

# Bulletin of the Museum of Comparative Zoology



Volume 162, Number 5

28 June 2019

## Ants of Grenada (Hymenoptera, Formicidae)

James K. Wetterer, David Lubertazzi, and Edward O. Wilson



HARVARD UNIVERSITY | CAMBRIDGE, MASSACHUSETTS, U.S.A.

# ANTS OF GRENADA (HYMENOPTERA, FORMICIDAE)

JAMES K. WETTERER,<sup>1</sup> DAVID LUBERTAZZI,<sup>2</sup> AND EDWARD O. WILSON<sup>2</sup>

**ABSTRACT.** On West Indian islands, as elsewhere in the world, ants are a very important component of virtually every terrestrial ecosystem. Nonetheless, the ants of most West Indian islands have remained largely unknown and unstudied. Now several destructive exotic ant species are spreading through the region, threatening native biodiversity. Here, we have compiled published and unpublished ant records and collected new specimens to document the diversity of ants on the island of Grenada. Our investigations increased the list of ant taxa known from the island to 82 (65 New World and 17 Old World species). Of these, 71 species are represented among specimens we collected, whereas 11 are New World species known from Grenada solely on the basis of earlier records. Some species recorded earlier, including at least nine not seen for more than 100 years, may now be extinct on Grenada. Grenada has more New World ant species than are known for Barbados (46), a neighboring island that has 34% more land area. Factors that may contribute to this difference include: 1) during low sea levels 15,000 years ago, Grenada was part of a larger island about 10 times Grenada's current size; 2) Grenada is more mountainous than Barbados; and 3) Grenada has more remaining forest cover than Barbados (50.0% vs. 14.7%). Conversely, Grenada has fewer Old World ant species than are known for Barbados (24). Factors that may contribute to this difference include: 1) lower human population density, 2) lower levels of imported lumber products, and 3) lower tourism levels. Records for only four of the 17 Old World exotic ants found in Grenada date to before 1995. Major tramp ant species that are known from the West Indies but have not yet been recorded from Grenada include Old World species such as the pharaoh ant (*Monomorium pharaonis*), the African big-headed ant (*Pheidole megacephala*), and the difficult white-footed ant (*Technomyrmex difficilis*), as well as the red imported fire ant (*Solenopsis invicta*).

**Key words:** Ants, Biogeography, Exotic species, Island biogeography, West Indies

## INTRODUCTION

The West Indies is recognized as a threatened "biodiversity hot spot" because of its high levels of biotic endemism (e.g., 58% of terrestrial plant species and 51% of terrestrial vertebrate species) and widespread habitat destruction (only 10–15% intact native vegetation remaining) (Solórzano et al., 2005). On West Indian islands, as elsewhere in the world, ants are a very important component of virtually every terrestrial ecosystem. Yet the native ants of most West Indian islands have remained largely unknown. Now several destructive exotic ant species are spreading through the region, threatening native invertebrate diversity. We have been conducting ant faunal inventories for all major islands of the eastern Caribbean to better understand and appreciate the biodiversity of this region.

Geographic isolation of species through tectonic movements and sea-level fluctuations, as well as immigration, extinction, and speciation, have all shaped the biota of the West Indies. Each island has a different balance of these forces related to the island's origin, age, topography, current and past size, and degree of access by potential biotic colonists. The result is a varied collection of natural experiments in island biogeography, with the main regions of the West Indies having fundamentally different biotas.

<sup>1</sup> Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, Florida 33458. Author for correspondence (wetterer@fau.edu).

<sup>2</sup> Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138.



Figure 1. Major islands ( $>50 \text{ km}^2$ ) of the eastern Caribbean. Unshaded areas are now submerged, but were dry land 25–15 kya when sea levels were  $\sim 120\text{--}140 \text{ m}$  lower.

The West Indies encompass five main regions: the Atlantic islands of the Florida–Bahama Platform, the three Caribbean island arcs of the Greater, Lesser, and Leeward Antilles, and the South American Shelf islands (Fig. 1). The islands in each of these regions show fundamental differences in origin, history, and topography (Duncan and Hargraves, 1984; Pindell and Barrett, 1990; Hedges, 2001). The Florida–Bahama Platform islands have an ancient continental foundation tectonically attached to North America since the Paleozoic. The three Caribbean island arcs formed around the edges of the Caribbean Plate, which originated west of present-day Central America in the Mesozoic and has since drifted northeastward and rotated counterclockwise

relative to North and South America. The proto-Greater Antilles first emerged above sea level  $>100$  million years ago (mya) (Smiley, 2002), and were closely associated with or attached to the Yucatan Platform until  $\sim 60$  mya. In contrast, the oldest Lesser Antilles emerged  $\sim 50\text{--}40$  mya as isolated oceanic islands. The Leeward Antilles and the South American Shelf islands first emerged  $\sim 90$  mya and have always remained closely associated with South America.

The biota of West Indian islands may be examined in the context of island biogeography theory, in terms of a dynamic balance of immigration and extinction (MacArthur and Wilson, 1967). Theory predicts that islands closer to source populations will

have higher immigration rates and larger islands will have lower extinction rates, both leading to higher equilibrium species richness. These effects are complicated in the West Indies, not only because of the multiple source populations to the south, west, and north, but also because the island sizes and distances to sources have changed greatly over time. Species on islands that have recently changed in size and connectivity would be expected to be in disequilibrium. Islands that were recently connected to a larger landmass should be “supersaturated,” i.e., with more species relative to their size compared with islands separated for a longer period or never connected (Wilcox, 1978). Over time, species richness should decrease until it eventually approaches the value expected for islands that were never part of a larger landmass.

Another process in island biogeography is the “oceanic filter” effect, where oceanic islands farther from continental source populations receive a lower diversity of colonists, resulting in a steady reduction in the number of species, genera, and families found on these islands (Wilson, 1961; Carlquist, 1965). In Oceania, where prevailing currents bring most immigrants from Australia and Southeast Asia, there is a decline in species richness from west to east across Melanesia, Micronesia, and Polynesia. The pattern in the West Indies, however, would be expected to be more complicated because of multiple source populations: South, Central, and North America. In addition, the large islands of the Greater Antilles serve as significant secondary sources. If one knows the geographic origin of different clades, however, one may examine filters of colonists from each source independently.

Wilson (1988) published preliminary biogeographic analyses of West Indian ants, including the fossil ant fauna of the Dominican amber (Wilson, 1985a,b,c,d,e; Baroni-Urbani and Wilson, 1987). In eval-

uating the geographic origin of West Indian ants, Wilson (1988) made the qualitative evaluation that most derived from species that island-hopped “to varying degrees of penetration from South America northward through the Lesser Antilles and in some cases onto the larger islands of the Greater Antilles.” In addition, Wilson (1988) recognized a set of species that “appears generally older, [and] comprises species endemic to one or more of the middle-sized to larger islands, especially the four major islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico).”

In our first published inventory, Wetterer et al. (2016) reviewed the known ant fauna of Barbados. Barbados is the fourth largest island of the Lesser Antilles (Fig. 1). Compared with other islands of the Lesser Antilles of similar size, we expected Barbados to have a relatively depauperate native ant fauna on the basis of several factors. First, Barbados is the most isolated island of the Lesser Antilles, far to the east of all other islands (Fig. 1). In addition, Barbados has never been connected to any other landmass, so all terrestrial species that have colonized Barbados had to cross the intervening ocean. Finally, compared with other major island in the Lesser Antilles, Barbados is flatter, more developed, and with less intact forest. Soon after European colonization in the 1600s, settlers quickly cleared most of the forest for agriculture. Conversely, we expected Barbados to be home to many exotic ant species, introduced throughout a long history of international commerce and tourism. Barbados has traditionally depended heavily on imports from abroad, notably lumber and other building material (Peterson, 1973).

In the present paper, we examine the ant fauna of the island of Grenada, the southernmost island of the Lesser Antilles. Although Grenada is not far from Barbados geographically, it differs in its geologic history, topography, geographic isolation, and in human impacts.



### Published Ant Records from Grenada

In the earliest report on ants in Grenada, John Castles (1790) wrote extensively about a population explosion of “sugar ants” that devastated Grenada beginning around 1770, but largely receded after a major hurricane in 1780. Although the identity of this plague ant remains unknown, Wheeler (1926) and Wilson (2005) concluded that it was probably *Solenopsis geminata* (Fabricius), which may have had a population explosion associated with a population of plant-feeding Hemiptera.

Herbert Huntington Smith (1851–1919), an American naturalist, collected biological specimens in the West Indies 1889–1895, commissioned by the Royal Society of London. Forel (1897) listed records of ants that Smith collected in Grenada in 1890 (here with current taxonomy): *Anochetus inermis* André, *Anochetus mayri* Emery, *Anochetus testaceus* Forel, *Brachymyrmex obscurior* Forel, *Camponotus opaciceps* Roger, *Camponotus sexguttatus grenadensis* Forel, *Cephalotes pallens* (Klug), *Crematogaster crinosa* Mayr, *Cyphomyrmex rimosus* Spinola, *Dorymyrmex pyramicus* Roger, *Leptogenys arcuata* Roger, *Monomorium ebeninum* Forel, *Monomorium floricola* (Jerdon), *Neivamyrmex antillanus* (Forel), *Neivamyrmex klugii* (Shuckard), *Odontomachus haematodus* (L.), *Odontomachus insularis* Guérin, *Paratrechina longicornis* (Latreille), *Paratrechina vividula antillana* (Forel), *Pheidole antillana* Forel, *Pheidole fallax* Mayr, *Pheidole sculptior* Forel, *Platythyrea punctata* Smith, *Pseudomyrmex flavidulus* (Smith), *Solenopsis castor* Forel, *S. geminata*, *Solenopsis globularia* Smith, *Strumigenys smithii* Forel, *Wasmannia auropunctata* (Roger), and *Wasmannia sigmaidea* Mayr. Forel (1897) wrote that all these species except *A. inermis* had also been found in St. Vincent and that the ant fauna of the two islands were almost identical. In addition, Wheeler (1910a) described one new species, *Nesomyrmex*

*clavipilis* Wheeler, on the basis of a specimen H. H. Smith collected in Grenada.

Charles T. Brues (1879–1955), working for the Museum of Comparative Zoology (MCZ), collected insects in Grenada in 1910. Wheeler (1911) listed 24 ant taxa that Brues collected in Grenada, including 10 valid taxa not previously recorded: *Anochetus emarginatus* (Fabricius), *Camponotus atriceps nocens* Wheeler, *Camponotus ustus* Forel, *Crematogaster laevis bruesi* Wheeler, *Leptogenys punctaticeps* Emery, *Linepithema iniquum* (Mayr), *Mycetophylax conformis* (Mayr), *Pseudoponera stigma* (Fabricius), *Pheidole bruesi* Wheeler, and *Pheidole jelskii* Mayr. Of the 41 ant species collected by Smith and Brues, only two were Old World exotic species (*Monomorium floricola* and *Paratrechina longicornis*).

Kempf (1960) added *Pseudomyrmex termitarius* (Smith) to the list of ants of Grenada. Kempf (1972), in his catalog of Neotropical ants, included records of all species known from Grenada in Forel (1897), Wheeler (1910a, 1911), and Kempf (1960), except two: *M. ebeninum* and *S. smithii* (both in Forel, 1897). Ward (1992) added two more species to the list of ants from Grenada: *Pseudomyrmex simplex* (Smith) and *Pseudomyrmex* PSW-52. Woodruff et al. (1998) summarized published records of ants from Grenada, but added no new records. Bolton (2000) reported *Strumigenys alberti* Forel from Grenada on the basis of H. H. Smith material. Seifert (2003) reported *Cardiocondyla emeryi* Forel from Grenada. Remarkably, this was only the third species of Old World exotic reported from Grenada.

Beginning in 2003, records of numerous additional individual ant species from Grenada have been published on the basis of our collections presented here (e.g., Wilson, 2003; Wetterer, 2009a,b,c, 2012a,b,c, 2014a,b, 2016, MacGown et al., 2012; Pacheco and Mackay, 2013; Wetterer and

Sharaf, 2017). Here, we present a full compilation of the known ants of Grenada.

## METHODS

We compiled published and unpublished ant records and collected new specimens to document the diversity of ants from Grenada. We searched for ant specimens from Grenada in the collection of the MCZ and the U.S. National Museum of Natural History (USNM). We also obtained records from the AntWeb site (AntWeb.org). Roland Thaxter (1858–1932), a Harvard mycologist, collected in Trinidad and Grenada in the winter of 1912–13; we found records of only two Grenada ant specimens that he collected.

Stefan P. Cover and Edward O. Wilson (C&W) collected ants in Grenada 14–21 June 1995 (with assistance from Philip Perkins); James K. Wetterer (JW) collected ants in Grenada 8–12 November 2003, 23–29 June 2006, and 2–9 July 2014. In addition, we obtained specimens collected in Grenada by Judith Endeman (JE) on 12 January 2005 and by Marco Mancini (MM) 16–19 April 2015. (See Appendix for site details.) C&W surveyed mainly in intact forest areas, and concentrated collecting on colonies, with each vial containing a single ant species. JW often surveyed in highly disturbed areas, including urban areas, collecting all ants encountered. JE and MM collected opportunistically in tourist areas.

Geocoordinates were originally estimates from a map. We later made small corrections to a few using Google Earth.

Stefan P. Cover identified most specimens from the 1995, 2003, 2005, and 2006 collections. JW identified most specimens from the 2014 and 2015 collections. José Pacheco and William Mackay identified most *Solenopsis* thief ants from 2003 and 2006 (Pacheco and Mackay, 2013). John LaPolla identified most *Nylanderia*. William Mackay identified most *Camponotus*. Mos-

tafa Sharaf identified the *Sylophopsis*. Philip Ward identified the *Pseudomyrmex*.

We classified each species as either New World or Old World and evaluated its known geographic range on the basis of information from multiple sources. When an ant species occurs in both the Old World and the New World, it is usually clear that one of these ranges is entirely exotic. Within a hemisphere, however, it is often much more difficult to evaluate what geographic area constitutes the native range and what area, in any, constitutes the exotic range. Although not all New World ants found in Grenada are necessarily native to the island, none is conclusively exotic to the island, i.e., introduced from another part of the New World through human commerce.

Kempf's (1972) catalog of Neotropical ants and Deyrup's (2003) checklist of Florida ants were particularly helpful sources of range information.

## RESULTS

We documented 82 ant species from the island of Grenada (65 New World and 17 Old World). Of these, 71 are represented among specimens we collected, and 11 are New World species only known from earlier records; Tables 1–4). In addition, Dark (1904 in Woodruff et al., 1998) reported that one additional species, *Acromyrmex octospinosus* (Reich), is found on Carriacou, an island in the Grenadines that is part of the nation of Grenada.

Published records appear to include some identification errors. We considered published records from Grenada of *Anochetus emarginatus*, *Camponotus ustus*, *Cyphomyrmex rimosus*, *D. pyramicus*, *O. haematodus*, *O. insularis*, and *Pheidole fallax* in Grenada to be misidentifications of *A. testaceus*, *Camponotus claviscapus* Forel, *Cyphomyrmex minutus* Mayr, *Dorymyrmex antillanus* Snelling, *Odontomachus bauri* Emery, *Odontomachus*

TABLE 1. NEW WORLD ANTS OF GRENADA COLLECTED IN PRESENT STUDY, LISTED BY DESCENDING NUMBER OF NEW SITE RECORDS.

	First <sup>a</sup>	New <sup>b</sup>	NW <sup>c</sup>			OW
<i>Solenopsis geminata</i>	1890	81	CST	bgv	LGBF	AfPaInAuOc
<i>Wasmannia auropunctata</i>	1890	78	CST	bgv	LGBF	AfPa—AuOc
<i>Cyphomyrmex minutus</i>	1890*	58	CST	bgv	LGBF	—
<i>Crematogaster crinosa</i>	1890	53	CST	bgv	LG—	—
<i>Odontomachus bauri</i>	1910*	50	CST	bgv	LG—	—
<i>Nylanderia</i> cf. <i>steinheili</i>	2003	49	CST	bgv	LGB—	—Pa—
<i>Brachymyrmex</i> cf. <i>obscurior</i>	1890	46	CST	bgv	LGBF	—AuOc
<i>Dorymyrmex antillanus</i>	1890*	44	—	—gv	LG—	—
<i>Pheidole jelskii</i>	1910*	33	—ST	bgv	LGB—	—
<i>Pheidole sculptior</i>	1890	32	CST	bgv	LG—	—
<i>Camponotus sexguttatus</i>	1890	31	CST	bgv	LGBF	—
<i>Monomorium ebeninum</i>	1890	27	CST	bgv	LGBF	—
<i>Anochetus mayri</i>	1890	26	CST	bgv	LGBF	—Pa—
<i>Pheidole flavens</i>	1890	26	CST	bgv	LGBF	—
<i>Rogeria foreli</i>	1995	25	CST	bgv	LG—	—
<i>Anochetus inermis</i>	1890	23	CST	bgv	LGB—	—
<i>Strumigenys margaritae</i>	2003	23	CST	bgv	LGBF	—
<i>Solenopsis globularia</i>	1890	22	CST	bgv	LGBF	—
<i>Crematogaster curvispinosa</i>	1995	23	CST	bgv	L—	—
<i>Odontomachus ruginodis</i>	1890*	19	CST	bgv	LGBF	—
<i>Camp. conspicuus sharpi</i>	1910*	19	C—	—gv	L—	—
<i>Hypoponera opacior</i>	2003	12	CST	—gv	LGBF	—
<i>Nylanderia</i> cf. <i>guatemalensis</i>	1890	12	CST	bgv	LGBF	—
<i>Pheidole antillana</i>	1890	11	—	—gv	L—	—
<i>Platythyrea punctata</i>	1890	11	CST	bgv	LGBF	—
<i>Strumigenys smithii</i>	1890	10	CST	—gv	L—	—
<i>Pheidole subarmata</i>	1995	9	CST	bgv	LGB—	—
<i>Solenopsis pollux</i>	2003	9	CS—	bgv	LG—	—
<i>Brachymyrmex</i> cf. <i>heeri</i>	2003	8	CST	bgv	LGBF	—Pa—
<i>Pseudoponera stigma</i>	1910	8	CST	bgv	LGBF	—
<i>Solenopsis azteca</i>	2003	8	CS—	bgv	LG—	—
<i>Strumigenys eggersi</i>	2006	7	CST	bgv	LGBF	—
<i>Rogeria curcubens</i>	2003	6	—ST	bgv	LGB—	—
<i>Pheidole bruesi</i>	1910	6	—	—gv	—	—
<i>Hypoponera opaciceps</i>	2003	6	CST	bgv	LGBF	—PaInAuOc
<i>Pseudomyrmex</i> PSW-52	1995	5	CS—	—g—	—	—
<i>Mycocepurus smithii</i>	2003	4	CST	—gv	LG—	—
<i>Neivamyrmex klugii</i>	1890	4	—ST	—gv	L—	—
<i>Anochetus testaceus</i>	1890	3	C—	—gv	—GB—	—
<i>Lachnomyrmex pilosus</i>	2003	3	—ST	—g—	—	—
<i>Prionopelta antillana</i>	1995	3	CST	—gv	LG—F	—
<i>Strumigenys elongata</i>	2006	3	CST	—gv	L—	—
<i>Linepithema iniquum</i>	1910	3	CST	—gv	LG—	—Pa—
<i>Mycetophylax conformis</i>	1910	2	—ST	—g—	LG—	—
<i>Camponotus claviscapus</i>	1910	2	CST	—gv	L—	—
<i>Solenopsis pygmaea</i>	2006	2	C—	bgv	—G—	—
<i>Nylanderia fulva/pubens</i>	2003	1	CST	bgv	LG—F	—
<i>Solenopsis castor</i>	1890	1	CS—	—gv	L—	—
<i>Solenopsis maboya</i>	2006	1	—	—g—	—G—	—
<i>Solenopsis zeteki</i>	2006	1	CS—	bg—	L—	—
<i>Strumigenys alberti</i>	1890	1	CS—	—gv	LG—	—
<i>Strumigenys silvestrii</i>	2006	1	—S—	—gv	—GBF	—
<i>Strumigenys subdentata</i>	1995	1	CST	—g—	—	—
<i>Nylanderia</i> n. sp.	1995	1	—	—g—	—	—

<sup>a</sup> First = earliest record; \* = first published record; uncertain identification or apparently misidentified.<sup>b</sup> New = no. of new site records (1995–2015).<sup>c</sup> New World Range (NW): C = Central America, S = South America, T = Trinidad, b = Barbados, g = Grenada, v = St. Vincent, L = other Lesser Antilles, G = Greater Antilles, B = Bahamas, F = Florida. Old World Range (OW): Af = Afrotropic, Pa = Palearctic, In = Indomalaya, Au = Australasia, Oc = Oceania.

TABLE 2. NEW WORLD ANTS OF GRENADA NOT COLLECTED IN PRESENT STUDY.<sup>a</sup>

	First	New	NW			OW
<i>Cephalotes pallens</i>	1890	0	CST	–gv	L—	—
<i>Crematogaster laevis bruesi</i>	1910	0	—	–g–	—	—
<i>Leptogenys arcuata</i>	1890	0	–ST	bgv	L—	—
<i>Leptogenys pubiceps</i>	1910 <sup>a</sup>	0	–ST	bgv	LGB–	—
<i>Nesomyrmex clavipilis</i>	1890	0	—	–g–	—	—
<i>Pachycondyla harpax</i>	1913	0	CST	–g–	LG—	—
<i>Pseudomyrmex flavidulus</i>	1890	0	CST	–gv	—	—
<i>Pseudomyrmex simplex</i>	<1992	0	CST	bgv	LGBF	—
<i>Pseudomyrmex termitarius</i>	<1960	0	CST	–gv	—	—
<i>Thaumatomyrmex</i> sp3	1890	0	–S–	–g–	—	—
<i>Wasmannia sigmoidea</i>	1890	0	CS–	–gv	LG—	—

<sup>a</sup> Symbols as in Table 1.

*ruginodis* Smith, and *P. jelskii*, respectively (see below).

Creighton (1930) incorrectly listed *Eciton commutatum* (Forel) (= *Neivamyrmex punctaticeps* (Emery)) as described from “Grenada B.W.I.”; this species was, in fact, described from New Grenada (= Colombia).

In total, 45 ant species had been documented from Grenada before our surveys (Tables 1–3): 30 from the specimens Smith collected in 1890, 10 from Brues’ 1910 collection, and five from various other surveys. Our four Grenada ant collections in 1995, 2003, 2006, and 2014 yielded an apparently diminishing number of previous-

ly unrecorded species, finding 11, 16, 7, and 2, respectively (Tables 1 and 3). The two new species records from 2014 were both Old World exotic species.

The numbers of known New World and Old World ant species from Barbados (Table 4) come from Wetterer et al. (2016), with a few changes. On the basis on identification by John LaPolla, we now divide *Nylanderia* cf. *steinheili* from Barbados into two species, *Nylanderia guatemalensis* and *Nylanderia steinheili*. Further, on the basis of identifications by Mostafa Sharaf, we now consider *Sylophopsis subcoeca* to be an Old World exotic. These

TABLE 3. OLD WORLD EXOTIC ANTS OF GRENADA.<sup>a</sup>

	First	New	NW			OW
<i>Paratrechina longicornis</i>	1890	46	CST	bgv	LGBF	AfPaInAuOc
<i>Tapinoma melanocephalum</i>	1995	30	CST	bgv	LGBF	AfPaInAuOc
<i>Trichomyrmex destructor</i>	2003	23	CST	bgv	LGBF	AfPaInAuOc
<i>Monomorium floricola</i>	1890	19	CST	bgv	LGBF	AfPaInAuOc
<i>Cardiocondyla mauritanica</i>	2003	17	—	bg–	–G–F	AfPaInAu—
<i>Tetramorium simillimum</i>	2003	15	CST	bgv	LGBF	AfPaInAuOc
<i>Hypoponera punctatissima</i>	2003	3	CS–	bg–	LGBF	AfPaInAuOc
<i>Cardiocondyla minutior</i>	1995	7	C–T	bgv	–GBF	Af—InAuOc
<i>Strumigenys rogeri</i>	2006	5	CST	bgv	LGBF	AfPaInAuOc
<i>Strumigenys emmae</i>	2006	4	CST	bgv	LGBF	Af—InAuOc
<i>Cardiocondyla obscurior</i>	2006	4	CS–	bg–	–G–F	AfPaInAuOc
<i>Cardiocondyla emeryi</i>	1935	3	CST	bgv	LGBF	AfPaInAuOc
<i>Tetramorium bicarinatum</i>	1918	3	CST	bgv	LGBF	AfPaInAuOc
<i>Sylophopsis subcoeca</i>	2014	3	—	bg–	LG—	—In—Oc
<i>Sylophopsis sechellensis</i>	2003	2	—	bgv	LG—	Af—InAuOc
<i>Plagiolepis alluaudi</i>	1995	2	—	bg–	LG–F	AfPaInAuOc
<i>Pheidole indica</i>	2014	1	–S–	bg–	LG—	AfPaIn—

<sup>a</sup> Symbols as in Table 1.



TABLE 4. ANT SPECIES RICHNESS OF GRENADA AND THE NEIGHBORING ISLANDS OF BARBADOS (WETTERER ET AL., 2016) AND ST. VINCENT (WETTERER, IN PREP.). ELEV. = MAXIMUM ELEVATION. NW = NEW WORLD SPECIES, OW= OLD WORLD SPECIES.

	Area (km <sup>2</sup> )	Elev. (m)	% Forest	Pop./km <sup>2</sup>	Tourists/yr	# Known Ant Species		
						NW	OW	Total
St Vincent	381	1,234	69.2	283	79k	70	15	85
Grenada	344	840	50.0	315	135k	65	17	82
Barbados	462	336	14.7	666	632k	46	24	70

changes result in a net increase in one Old World ant species in Barbados. The numbers of New World and Old World species known from St. Vincent (Table 4), are based primarily on specimens that H. H. Smith collected in 1889–90, and that JW collected in 2004 and 2006 (Wetterer, in prep.).

SPECIES ACCOUNTS

Collectors: HS = Herbert H. Smith in 1890. CB = Charles T. Brues in 1910. C&W = Stefan P. Cover and Edward O. Wilson in 1995. JW = James K. Wetterer in 2003, 2006, and 2014. JE = Judith Endeman in 2005. MM = Marco Mancini in 2015. + = earliest specimens for Grenada collected in the present study. \* = reidentification. Published records include site information only for specimens not collected in the present study. Numbers in parentheses refer to vial numbers listed in the Appendix, with underlines grouping vials from the same site.

1. *Anochetus inermis* André

*Published Records.* No site data (HS; Forel, 1897). Sauteurs (CB; Wheeler, 1911). *New Specimens.* C&W, three sites (G32, G125, G155). JW, 19 sites (2003: 17, 22; 2006: 462, 466, 500, 501, 531, 538, 557; 2014: 204, 209, 214, 215, 244, 258, 260, 289, 305, 309). MM, one site (119).

We found this tawny to yellow trap-jaw ant in both natural and highly disturbed habitats. *Anochetus inermis* is known from northern South America and many islands in the West Indies (Wetterer et al., 2016).

2. *Anochetus mayri* Emery

*Published Records.* No site data (HS; Forel, 1897). *New Specimens.* C&W, four sites (G72, G111, G130, G142). JW, 22 sites (2003: 2, 3–4, 11, 12, 25, 34, 36, 38, 39, 40; 2006: 462, 466, 485, 548; 2014: 209, 219, 227, 260, 289, 296, 311, 316, 320).

This trap-jaw ant is smaller and darker than the other *Anochetus* species present in Grenada. We found this species in both natural and highly disturbed habitats. *Anochetus mayri* is common in many parts of its range in South America, Central America, and the West Indies. *Anochetus mayri* has invaded Florida and the Bahamas, and is now widespread in peninsular Florida, commonly nesting within deep litter at the base of pine trees (Wetterer et al., 2018).

3. *Anochetus testaceus* Forel

*Published Records.* No site data (HS; Forel, 1897 as *Anochetus emarginatus testaceus*). Grand Etang (CB; Wheeler 1911 misidentified as *A. emarginatus* (Fabricius); USNM reidentified). *Unpublished Record.* Grand Etang (R. Thaxter, California Academy of Sciences Collection, det. W. L. Brown; CASENT0217513). *New Specimens.* C&W, two sites (G20, G86, G99). JW, one site (2006: 523–527).

This long, thin, New World trap-jaw ant is the largest of the three *Anochetus* species we found in Grenada. We collected this species only at three relatively undisturbed forest areas. In Puerto Rico, Wheeler (1908) reported finding colonies nesting under stones in shaded areas of dry arroyos.

Wheeler (1911) misidentified three workers of *A. testaceus* as *A. emarginatus*. These specimens at the USNM have been reidentified by an unnamed subsequent researcher.

#### 4. and 5. *Brachymyrmex* spp.

*Brachymyrmex* are small, chubby New World ants that range in color from light yellow to dark brown. They are particularly prevalent in disturbed habitats, and are often common in areas dominated by invasive ants.

The taxonomy of the West Indian *Brachymyrmex* species is problematic. The two most commonly applied names, *Brachymyrmex heeri* Forel and *B. obscurior* Forel, have been reported from many of the islands. For example, Torres and Snelling (1997) listed just these two as the only *Brachymyrmex* species from Puerto Rico and the Virgin Islands. In the paper of Wetterer et al. (2016) on the ants of Barbados, Stefan Cover separated our *Brachymyrmex* specimens into two forms: *B. cf. heeri* and *B. cf. obscurior*. He split our Grenada specimens into the same two categories. Claudia Ortiz, however, examined a subset of our Grenada specimens and divided them into five species: *B. heeri* and *B. obscurior*, plus *Brachymyrmex corde-moyi* Forel, *Brachymyrmex patagonicus* Mayr, and *Brachymyrmex minutus* Forel.

Unfortunately, it is unclear to us which forms should be given these different names, or what distinctive morphological features can be used to make reliable determinations (see Deyrup, 2016; Lubertazzi, 2019). Although there are at least two species of *Brachymyrmex* among our Grenada specimens, we remain uncertain of their taxonomy.

#### 4. *Brachymyrmex cf. heeri*

*New Specimens.* JW, eight sites (2003: 15, 34, 397; 2006: 462, 482, 485, 490; 2014: 227).

#### 5. *Brachymyrmex cf. obscurior*

*Published Records.* No site data (HS; Forel, 1897 as *Brachymyrmex heeri obscurior*).

*Unpublished Records.* Pearls, Saline, and St. George's (N. Krauss; USNM).

*New Specimens.* C&W, one site (G63). JW, 45 sites (2003: 2, 5, 9, 18, 24, 26, 27, 29, 30, 37; 2006: 466, 470, 481, 490, 494, 497, 501, 505, 507, 531, 536, 537, 553, 563, 572; 2014: 208, 213, 215, 239, 242, 256, 258, 267, 269, 272, 273, 278, 279, 280, 283, 284, 288, 289, 305, 306, 310). MM, two sites (119, 121).

#### 6. *Camponotus (Pseudocolobopsis) claviscapus* Forel

*Published Records.* Grand Etang (CB; Wheeler, 1911 misidentified as *Camponotus ustus* Forel; USNM; reidentified by JW).

*New Specimens.* JW, two sites (2003: 25; 2006: 487).

*Camponotus claviscapus*, a yellow-brown carpenter ant, is known from South and Central America, as well as Trinidad. In the Lesser Antilles, JW (unpublished) has also collected this species on St. Vincent, St. Lucia, and Martinique. *Camponotus claviscapus* commonly nests in hollow twigs. *Camponotus claviscapus occultus* Wheeler & Mann is known from Haiti and the Dominican Republic (Lubertazzi, 2019). *Camponotus claviscapus* appears similar to *Camponotus (Pseudocolobopsis) fugax* Forel of Jamaica and *Camponotus (Pseudocolobopsis) kaura* Snelling & Torres of Puerto Rico and the Virgin Islands.

Wheeler (1911) misidentified two minors of *C. claviscapus* as *C. ustus*, a species known from Hispaniola, Puerto Rico, and the Virgin Islands (Snelling and Torres 1998). The minors of these two species are similar, but the majors of *C. claviscapus* have narrower heads with parallel sides.

**\*7. *Camponotus (Tanaemyrmex) conspicuus sharpi* Forel**

*Published Records.* No site data (Forel, 1897 as *Camponotus abdominalis opaciceps*). Grand Etang (1910; CB; Wheeler, 1911 as *C. abdominalis nocens*; MCZ). Richmond Hill (CB; Wheeler, 1911 as *C. abdominalis nocens*; MCZ).

*New Specimens.* C&W, two sites (G14, G49). JW, 15 sites (2003: 21, 25, 33, 35; 2006: 471–480, 488–489, 503, 508–516, 522, 540–547, 2014: 223, 235, 250, 265, 289, 300). MM, two sites (122, 124).

Forel (1897) reported *C. abdominalis opaciceps* (= *C. opaciceps*) from Grenada, writing that it was very close to *Camponotus sharpi* (= *C. conspicuus sharpi*) of St. Vincent. Wheeler (1911) described *C. abdominalis nocens* (= *C. atriceps nocens*) from Grenada, but noted: “perhaps *nocens* should be regarded merely as a variety of *sharpi*, rather than as an independent subspecies.” Hashmi (1973) synonymized many *C. abdominalis* subspecies with *C. abdominalis* (= *C. atriceps*), but considered both *opaciceps* and *nocens* to be “taxa of uncertain status.” Hashmi (1973) examined specimens that Forel identified as *C. opaciceps* from Venezuela and “Grenador” (no doubt a misreading of “Grenada”), and wrote: “The above specimens from the Forel Collection do appear to be typical of *abdominalis*. Since I have no verifiable specimens of *opaciceps*, the status of this taxon will remain uncertain until I have examined the type specimen or else have some additional material which fits Roger’s description.” Concerning *nocens*, Hashmi (1973) wrote: “Based on Wheeler’s description and on my examination of the specimens in the Creighton Collection, it seems evident that this taxon is not closely related to *abdominalis* and probably does not belong in the subgenus *Myrmothrix*. This taxon then is accorded uncertain status until the type material can be located and examined.” Thus, on the basis of Hashmi

(1973), perhaps one could conclude that there are two different enormous *Camponotus* in Grenada, one (*C. opaciceps*) that is synonymous with *C. atriceps* and the other (*C. atriceps nocens*) that is probably in a different subgenus from *C. atriceps*. Until a regional revision of *Camponotus* is done, we will refer to all our specimens of giant carpenter ants from Grenada as *C. (Tanaemyrmex) conspicuus sharpi*, a taxon that both Forel (1897) and Wheeler (1911) agreed was close to the specimens they examined.

**\*8. *Camponotus (Myrmothrix) sexguttatus* (Fabricius)**

*Published Records.* No site data (HS; Forel, 1897). Grand Etang (CB; Wheeler, 1911 as *C. sexguttatus grenadensis*). Richmond Hill (CB; Wheeler, 1911 as *C. sexguttatus grenadensis*).

*New Specimens.* C&W, three sites (G40, G70, G144). JW, 28 sites (2003: 4, 13, 14, 21, 33, 35, 38; 2006: 462, 463, 467, 481, 482, 484, 493, 502, 520–521, 522, 548, 550, 560–561, 564, 566–568, 573, 579–580; 2014: 207, 233, 250, 293, 314, 319, 320).

The widespread New World carpenter ant *C. sexguttatus* commonly nests inside dead branches, in hollow twigs, under bark, and in dead wood. It is abundant in many habitats and is often found in open disturbed habitats.

Most *C. sexguttatus* workers and queens from Grenada have a lighter-colored head and thorax than the typical form in many other parts of its range, elsewhere referred to as *C. sexguttatus grenadensis* or *C. sexguttatus biguttatus* (see below). As with our Barbados specimens (Wetterer et al., 2016), we have not separated out lighter forms on our list of *C. sexguttatus*. In Barbados and Grenada, the lighter form predominated in our samples, whereas in St. Vincent, the dark typical form is more common (Wetterer, in prep.).

Forel (1897) described *C. sexguttatus grenadensis* from Barbados and Grenada. Emery (1898) considered *grenadensis* to be a junior synonym of *Camponotus biguttatus* Emery (= *C. sexguttatus biguttatus*), a subspecies otherwise known only from Bolivia. Wheeler (1923), however, placed *biguttatus* as a subspecies of *sexguttatus* and separated it from *grenadensis* and all other subspecies of *sexguttatus* in the first couplet of his dichotomous key. Wheeler (1923) wrote that *biguttatus* was the sole subspecies with “epinotum [= mesosoma] in profile convex and arcuate above”; all other subspecies have “epinotum in profile straight or more or less depressed above.” Wheeler (1923) also described two additional subspecies of *sexguttatus* from the Lesser Antilles, both of which have lighter head, thorax, and gaster than the typical form: *antiguensis* Wheeler from Antigua (“gaster with cream-colored spots on second segment”) and *montserratensis* from Montserrat (“gaster immaculate”). Emery (1925), in his catalog of known ants, listed *biguttatus* as a variety of *seguttatus* and with *grenadensis* as a junior synonym of *biguttatus*. Emery (1925), however, did not consider *antiguensis* and *montserratensis*, so presumably he had not read Wheeler (1923) and did not know the characters Wheeler (1923) used to separate *biguttatus* and *grenadensis*. Nonetheless, Bolton (2018a,b) listed *antiguensis* and *montserratensis* as valid subspecies, but listed *grenadensis* as a junior synonym of the Bolivian *biguttatus*. Following Wheeler (1923), Wetterer et al. (2016) did not consider *grenadensis* to be a junior synonym of *biguttatus*. Although *grenadensis* specimens are strikingly lighter in color than the typical form, genetic analyses should examine whether these should be considered distinct species.

### 9. *Cardiocondyla emeryi* Forel

*Published Records.* No site data (Seifert, 2003; 1935; N. Weber; MCZ; det. B. Seifert).

*New Specimens.* C&W, two sites (G37, G158). JW, one site (2006: 552).

*Cardiocondyla emeryi*, an African native, is a well-known cosmopolitan tramp species distributed worldwide by human commerce (Wetterer, 2012d). This species is most common in disturbed environments and often co-occurs with dominant exotic ant species (Wetterer, 2012d). Because of their very small size, all *Cardiocondyla* species are probably often overlooked. There are currently 72 described *Cardiocondyla* species, all native to the Old World. Although many of these species are difficult to differentiate, the six species known from the New World are relatively easy to separate.

### +10. *Cardiocondyla mauritanica* Forel

*Published Records.* Wetterer (2012e).

*New Specimens.* JW, 17 sites (2003: 16, 26, 30, 37; 2006: 468, 481, 482, 490, 494, 505, 517, 528, 536, 537, 550, 553, 572).

*Cardiocondyla mauritanica* is an African native that has become a cosmopolitan tramp species (Wetterer, 2012e). In the New World, many older studies recorded this species as its junior synonym, *Cardiocondyla ectopia* Snelling. This species is most common in disturbed environments.

### +11. *Cardiocondyla minutior* Forel

*Published Records.* Wetterer (2014b).

*New Specimens.* C&W, one site (G45). JW, six sites (2003: 5, 41; 2006: 462, 463, 505; 2014: 289).

*Cardiocondyla minutior* is an Indo-Malayan native that has become a cosmopolitan tramp species (Wetterer, 2014b). In the New World, many older studies incorrectly recorded this species as *Cardiocondyla nuda* (Mayr). *Cardiocondyla minutior* was reported as nesting in shallow soil in open, disturbed areas with bare or weakly herbaceous ground cover (Seifert, 2003).



**+12. *Cardiocondyla obscurior* Wheeler**

*Published Records.* None.

*New Specimens.* JW, four sites (2006: 497; 2014: 273, 284, 305).

*Cardiocondyla obscurior* is an Old World tramp species (Seifert, 2003). This species is often misidentified as another tramp, *Cardiocondyla wroughtonii* (Forel), but may be distinguished from this species on the basis of coloration and discriminant function analysis (Seifert, 2003). These two species also show ecological differences. *Cardiocondyla obscurior* is typically found foraging on and nesting up in vegetation and *C. wroughtonii* is collected on the ground level and found nesting in the soil. *Cardiocondyla obscurior* has been found nesting in a variety of cavities in bushes and trees. Colonies can be polygynous, and both alate and ergatoid males are known (Seifert, 2003).

**13. *Crematogaster crinosa* Mayr**

*Published Records.* No site data (HS; Forel, 1897 as *Crematogaster brevispinosa minutior*). Richmond Hill (CB; Wheeler, 1911 as *C. brevispinosa*). Grand Etang (CB; Wheeler, 1911 as *C. brevispinosa*).

*Unpublished Records.* Greenville (1941; EMcC Callen; USNM).

*New Specimens.* C&W, two sites (G31, G78, G108). JW, 47 sites (2003: 7, 8, 9, 10, 17, 18, 24, 25, 26, 29, 30, 37, 41; 2006: 468, 481, 482, 490, 494, 506, 507, 528, 531, 536, 553, 562, 563, 564–566, 569–570, 572, 579; 2014: 206, 210, 215, 239, 241, 250, 257, 269, 287, 293, 303, 306, 308, 309, 310, 311, 316). JE, one site (F2). MM, three sites (121, 122, 123).

Longino (2003) recorded this species from the West Indies (Grenada, Nevis, and St. Vincent) and from many sites in South and Central America, north to Texas: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Guyana, Mexico, Panama, Paraguay, Peru, Uruguay, Texas, and Venezuela. This was the most commonly collected ant

species in Barbados (Wetterer et al., 2016), both in forests and disturbed habitats, often occurring in very high densities. We most often found this species nesting in trees, but it also nests in the ground. Longino (2003) wrote that *C. crinosa*: “can form large, polydomous colonies that fill the available nesting cavities in the trees they inhabit. This ant is common in seasonally dry habitats but is also found in some wet forests, e.g., in disturbed areas and man-groves.”

**+14. *Crematogaster curvispinosa* Mayr**

*Published Records.* None.

*New Specimens.* C&W, one site (G114, G135). JW, 22 sites (2003: 4, 11, 12, 25, 26, 28, 38; 2006: 462, 463, 466, 486, 504, 522, 539–540, 548, 579; 2014: 213, 227, 250, 260, 306, 320).

Longino (2003) reported this species from the West Indies (St. Lucia) and from many sites in South and Central America, north to Mexico (Bolivia, Brazil, Colombia, Costa Rica, Guatemala, Guyana, Mexico, Nicaragua, Panama, Peru, and Venezuela). In the West Indies, this species has also been reported from Martinique (Forel, 1893, 1912), St. Vincent (Forel, 1893), and Barbados (Wetterer et al., 2016). Longino (2003) found that this species was most common in disturbed habitats, and “forms small monogynous colonies, with just a few dozen workers. Nests are made in any available small cavity of dead or live plants.”

**15. *Cyphomyrmex minutus* Mayr**

*Published Records.* No site data (HS; Forel, 1897 misidentified as *Cyphomyrmex rimosus*). Richmond Hill (CB; Wheeler, 1911 misidentified as *C. rimosus*).

*New Specimens.* C&W, three sites (G2, G11, G47, G59, G95, G102). JW, 55 sites (2003: 2, 4, 10, 11, 12, 17, 25, 28, 34–36, 38, 39, 40; 2006: 462, 463, 466, 468, 481, 485, 490, 494, 497, 500, 501, 507, 522, 531, 538,

539–540, 548, 550, 552, 553, 557, 562, 564, 569, 572, 573, 579; 2014: 209, 213, 215, 227, 239, 240, 251, 261, 272, 284, 289, 305, 306, 312, 318, 322).

*Cyphomyrmex minutus* is common across the West Indies, though it has often been misidentified as *C. rimosus* (see Wetterer et al., 2016). This small and inconspicuous fungus-growing ant freezes when disturbed and often may be overlooked. Mature colonies typically contain a few hundred workers and nest under or within material on the ground, including under bark, within decomposing wood, and under stones (Wheeler, 1905; Lubertazzi, 2019).

#### \*16. *Dorymyrmex antillanus* Snelling

*Published Records.* No site data (HS; Forel, 1897; misidentified as *Dorymyrmex pyramicus*). Sauteurs (CB; Wheeler, 1911; misidentified as *D. pyramicus*).

*New Specimens.* C&W, two sites (G24, G38). JW, 40 sites (2003: 6, 7, 8, 9, 16, 18, 20, 23, 24, 27, 29, 37, 41; 2006: 481, 494, 499, 500, 505, 536, 537, 538, 553, 563, 572; 2014: 204, 208, 209, 213, 256, 259, 267, 269, 273, 278, 279, 286, 289, 292, 306, 308, 310). JE, one site (F4). MM, one site (120).

This pyramid ant is known from the Greater and Lesser Antilles. *Dorymyrmex antillanus* is a common and abundant species in open, sunny areas on many Caribbean islands. *Dorymyrmex antillanus* nest entrance is usually surrounded by a small conic mound. This species, like others in the genus, can often be found foraging even during the hottest part of the day (Lubertazzi, 2019).

#### 17–19. *Hypoponera* spp.

*Unidentified New Specimens.* C&W, three sites (G5, G88, G104). JW, 14 sites (2003: 1, 2, 3, 17, 25, 28, 30; 2006: 466, 522, 540, 569; 2014: 208, 242, 289). MM, one site (121).

*Hypoponera* are small, subterranean ants that feed on minute soil arthropods. Typically forming small nests, their colonies can be found in rotten wood, leaf litter, under objects on the ground, and in the soil (Schmidt and Shattuck, 2014). *Hypoponera* can be abundant in areas with a well-developed, moist vegetative ground litter. *Hypoponera* species do not exhibit much morphological variation; hence the genus is rife with taxonomic issues and challenges making species determinations. There is a need for a West Indian generic revision to clarify what species are present, to establish clear species boundaries, and to establish if there is a means to make determinations using morphological features.

There are at least three *Hypoponera* species present in Grenada. JW distinguished three *Hypoponera* species from Grenada on the basis of mesopleuron shininess and petiole shape, and tentatively assigned them names that have widespread records in the West Indies as follows: *Hypoponera opaciceps*—all or mostly matte mesopleuron, relatively thick, box-like petiole with parallel front and rear faces in lateral view; *Hypoponera opacior*—matte mesopleuron, petiole with distinctly nonparallel curving front and flat rear faces narrowing toward the apex in lateral view; *Hypoponera punctatissima*—shiny mesopleuron, petiole with slightly nonparallel front and rear faces narrowing above. Most of the remaining *Hypoponera* specimens had petioles like *H. punctatissima*, but the mesopleuron was not completely shiny. Two additional *Hypoponera* species have been reported from St. Vincent: *Hypoponera foeda* and *Hypoponera ergatandria*. *Hypoponera foeda* is known only from St. Vincent (Forel, 1897). Bolton and Fisher (2011) considered *H. ergatandria* to be a junior synonym of *H. punctatissima*, but Seifert (2013) deemed it a separate species, most easily

distinguished from *H. punctatissima* by its shorter antennal scapes.

**+17. *Hypoconera opaciceps* (Mayr)**

*Published Records.* None.

*New Specimens.* JW, six sites (2003: 36; 2006: 485, 539; 2014: 250, 311, 316).

This New World species has an extremely broad distribution. Smith (1936) wrote that *H. opaciceps* “ranges from as far north as Boulder, Colorado, in the United States to as far south as Uruguay, South America, and throughout the islands of the West Indies.” In addition, *H. opaciceps* has spread to many Old World sites through human commerce.

**+18. *Hypoconera opacior* (Forel)**

*Published Records.* None.

*New Specimens.* JW, 12 sites (2003: 2, 4, 25, 34, 36, 38, 39; 2006: 466, 468, 482; 2014: 227, 316).

This New World species has an extremely broad distribution in South, Central, and North America and the West Indies. In addition, *H. opaciceps* has spread to a few Old World sites through human commerce.

**+19. *Hypoconera punctatissima* (Roger)**

*Published Records.* None.

*New Specimens.* JW, three sites (2003: 36; 2006: 506, 573).

Originally from the Old World, *H. punctatissima* has spread around the world through human commerce. Bolton and Fisher (2011) wrote: “*H. punctatissima* is without doubt the world’s most accomplished ponerine tramp-species.” *Hypoconera punctatissima* has been most commonly recorded in Africa and Europe, with a large distributional gap in the Sahara. Its relatively continuous distribution through sub-Saharan Africa supports the contention that *H. punctatissima* is native to this region, though *H. punctatissima* may also be native to subtropical parts of Europe, North Africa, or the Middle East.

With the globalization of human commerce, populations of *H. punctatissima* became established in many other regions of the world. Records of this species, however, are not yet known from large parts of the world, including most of continental Asia and Australia. It is unclear whether *H. punctatissima* has not yet reached these areas, has arrived but has been outcompeted by local species, or has simply remained undetected.

**+20. *Lachnomyrmex pilosus* Weber**

*Published Records.* None.

*New Specimens.* JW, three sites (2003: 3–4; 2014: 250, 316).

Except for records from Trinidad, these are the only records of this species outside of continental South and Central America. Little is known about the biology of this species. *Lachnomyrmex pilosus* is usually found in leaf litter samples, typically only one or two individuals at a time. A lack of nest collections, or even known collections of more than a few workers, suggests that they form small colonies, with foraging carried out by individual workers (Feitosa and Brandão, 2008).

**21. *Linepithema iniquum* (Mayr)**

*Published Records.* Grand Etang (CB; Wheeler, 1911; Wild, 2007; CASENT0013941; MCZ). Sauteurs (CB; Wheeler, 1911; Wild, 2007; CASENT0014044; MCZ).

*New Specimens.* C&W, one site (G23). JW, two sites (2003: 12–13, 2014: 231).

This widespread Neotropical species is known through Central America, South America, and the West Indies. This species is most commonly found nesting in trees, with colonies using whatever suitable cavities are available, e.g., dead wood on a live plant, bromeliads, and hollow vines. They will also nest in downed material on the ground, although foraging is mostly done above ground level. Nests can also be found in fields and along roadsides but this is

mostly a species of forested habitats. Like other *Linepithema*, its foragers are general scavengers that will also tend scale insects (Wild, 2007; Escarraga and Guerrero, 2016).

## 22. *Monomorium ebeninum* Forel

*Published Records.* No site data (HS; Forel, 1897 as *Monomorium minutum ebeninum*). No site data (DuBois, 1986).

*New Specimens.* C&W, two sites (G35, G48, G52, G57, G60). JW, 24 sites (2006: 466, 468, 494, 500, 504, 506, 507, 531, 533, 536, 539–540, 552, 553, 557, 562, 572; 2014: 204, 208, 209, 256, 267, 272, 279, 280, 306). MM, one sites (121).

*Monomorium ebeninum* is a small black ant with a widespread distribution in the West Indies, Central America, and Mexico, as well as southernmost Texas and Florida (Wetterer, 2017). This species has also been collected from several sites in the Florida Keys, where Deyrup et al. (2000) considered it to be exotic. However, the northernmost records of *M. ebeninum* in the Florida Keys and the Bahamas are at the same latitude (25.1°N), which is at the northern edge of an essentially continuous range through the West Indies. If *M. ebeninum* is native in the Bahamas, then there is little justification for considering populations immediately to the west, in the Florida Keys, to be exotic (Wetterer, 2017). This species occurs in a variety of habitats, particularly in coastal areas. Nests can be found in dead wood, under stones, and in a range of preformed cavities. Foragers are omnivorous and colonies can be polygynous.

## 23. *Monomorium floricola* (Jerdon)

*Published Records.* No site data (HS; Forel, 1897; Bolton, 1987). Sauteurs (CB; Wheeler, 1911).

*New Specimens.* No site data (1888; HS, British Museum of Natural History [BMNH]). C&W, two sites (G65, G153). JW, 17 sites (2003: 15, 27, 28; 2006: 466,

490, 500, 505, 507, 528, 538, 564; 2014: 208, 267, 269, 272, 281, 296).

The flower ant, *M. floricola*, native to Asia, is one of the most widely distributed ants of the tropics and subtropics. Occasionally, it is also found in temperate areas in greenhouses and heated buildings (Wetterer, 2010). Nests are typically above the ground, in cavities such as tree bark or in dead twigs and branches, and colonies can be polydomous. This species is rarely considered a serious pest. However, because this species is very small, slow moving, cryptically colored, and primarily arboreal, it is probably often overlooked and its abundance and ecological importance are underappreciated. *Monomorium floricola* may be particularly significant in flooded mangrove habitats, where competition with nonarboreal ants is much reduced (Wetterer, 2010). Queens are wingless and form new colonies by budding. This latter characteristic, coupled with polygyny, allows them to be readily transported and invade new areas (Deyrup et al., 2000).

## 24. *Mycetophylax conformis* (Mayr)

*Published Records.* Point Saline (CB; Wheeler, 1911).

*New Specimens.* JW, two sites (2003: 18; 2006: 505).

This dark brown fungus-growing ant is known from South America and the Greater and Lesser Antilles. Their ground nests are often located in sandy soil along the coast. The nest entrance is a small circular opening surrounded by a small mound. Their fungus gardens are relatively small (~250 ml), with one to three gardens per nest, and located in chambers from 15–50 cm below ground. Colony size was less than 600 individuals and contain a single queen (Klingenberg et al., 2007).

## +25. *Mycocrepurus smithii* Forel

*Published Records.* None.



*New Specimens.* JW, four sites (2003: 32; 2006: 481; 2014: 227, 250).

This light brown fungus-growing ant is widespread South and Central America and the Greater and Lesser Antilles. Nests of this soil-nesting species are often marked by a soil turret, though turretless nest entrances are also sometimes found at the edge of a stone. Nest chambers are only a few centimeters in diameter, but may be found up to a meter below ground. Colonies are polygynous, queens in some populations have been shown to develop through asexual parthenogenesis. Vegetation, caterpillar frass, and bat guano are known to be used as a substrate for their fungus (Rabeling et al., 2007).

## 26. *Neivamyrmex klugii* (Shuckard)

*Published Records.* No site data (HS; Forel, 1897). No site data (HS; Forel, 1897; as “? *Eciton klugi* ? *E. antillanum*”).

*Unpublished Site Record:* Balthazar (HS; labeled “*Eciton klugi* Shuck (*antillanum* For)”); CASENT0902655).

*New Specimens.* C&W, one site (G28). JW, three sites (2003: 4; 2006: 529–530, 562).

Shuckard (1840) described the army ant *Labidus klugii* (= *N. klugii*) from St. Vincent solely on the basis of male specimens. Forel (1897) reported males of *N. klugii* from Grenada, and described *Eciton antillanum* (= *Neivamyrmex antillanus*) from Grenada solely on the basis of workers, but wrote that it was likely that these were the workers of *N. klugii*. Most researchers since then have assumed that these two names refer to only a single species, and use the older name *klugii*. Nonetheless, *N. antillanus* has remained a valid name. *Neivamyrmex klugii* has also been reported from Trinidad and Tobago and Venezuela. *Neivamyrmex klugii distans* Borgmeier was described from Costa Rica, and remains only known from males. Gordon Snelling identified a worker specimen of *Neivamyrmex* from Monte-

verde, Costa Rica as *N. antillanus* (Ant-Web), though, on the basis of the collection locale, it seems likely that this is the same species as *N. klugii distans*.

**27.–29. *Nylanderia* spp.** *Unidentified New Specimens.* C&W, five sites (G8, G9, G13, G15, G18, G74, G76, G89, G98, G106, G110, G115, G123, G129, G131, G133, G148).

*Nylanderia* species are commonly called crazy ants, because of the foragers' rapid, seemingly erratic movements as they search for food. John LaPolla is currently revising the taxonomy of West Indian *Nylanderia*. LaPolla confirmed the identities of most of our Grenada *Nylanderia* specimens.

*Nylanderia fulva* (Mayr) and *Nylanderia pubens* (Forel) are New World species that have been reported from numerous sites scattered across the New World tropics and subtropics. Unfortunately, almost all records of are of questionable reliability because of problems with distinguishing *N. fulva* workers from *N. pubens* workers (Trager, 1984; Gotzek et al., 2012). *Nylanderia fulva* and *N. pubens*, however, may be distinguished using genetic analyses and male morphology (Gotzek et al., 2012).

*Nylanderia guatemalensis* and *Nylanderia steinheili* are similar in appearance and behavior. Both species have been reported primarily from Central America, the West Indies, and Florida. In the Lesser Antilles, we used the following characters based on color to separate the two species: *N. cf. steinheili*: overall body distinctly brown with contrasting white meso/metacoxae, and *N. cf. guatemalensis*: body yellow with contrasting darker macrosetae. One problem with using color as the distinguishing characteristic is that workers of different age can have different color and mode of specimen preservation can affect color, with specimens often bleaching over time. Both species inhabit a variety of habitats. Both nest in soil, and in and under dead wood.

+27. *Nylanderia fulva* (Mayr)/*Nylanderia pubens* (Forel)

*Published Records.* None.

*New Specimens.* JW, one site (2003: 31).

*Nylanderia fulva* has undergone population explosions in parts of Colombia, the southern U.S., and on St. Croix, U.S. Virgin Islands, where locals blamed *N. fulva* for serious crop damage, e.g., a coconut plantation produced no coconuts because of high densities of plant-feeding Hemiptera tended by the ants (Wetterer and Keularts, 2008). A pattern of an extreme population boom followed by a bust may be a common characteristic of *N. fulva* and might distinguish this species from *N. pubens* (Wetterer et al., 2014).

28. *Nylanderia* cf. *guatemalensis* (Forel)

*Published Records.* No site data (HS; Forel, 1897 as *Prenolepis guatemalensis antillana*).

*New Specimens.* C&W, two sites (G6, G46). JW, 10 sites (2003: 2–4, 17, 35, 40; 2014: 210, 228, 264, 296, 312, 321).

+29. *Nylanderia* cf. *steinheili* (Forel)

*Published Records.* None.

*New Specimens.* JW, 48 sites (2003: 2, 3–4, 25, 11, 12, 15, 40, 16, 17, 18, 26, 28, 30–32, 34, 38, 39; 2006: 462, 463, 466, 468, 481, 482, 485–486, 490, 501, 507, 517, 522, 539–540, 548, 552, 557, 564, 565, 569, 579; 2014: 210, 219, 228, 241, 251, 256, 272, 278, 291, 296, 302, 312, 317, 321). MM, one site (123).

+30. *Nylanderia* n. sp.

*Published Records.* None.

*New Specimens.* C&W, known from a single collection (G148).

One collection of this soon-to-be-described species (J. LaPolla, personal communication) was taken from a rotten stick on the ground in a nutmeg–banana plantation.

\*31. *Odontomachus bauri* Emery

*Published Records.* No site data (HS; Forel, 1897 misidentified as *O. haematodes*). Richmond Hill (CB; Wheeler, 1911 misidentified as *O. haematodes*).

*New Specimens.* C&W, three sites (G3, G16, G77, G81, G97, G126). JW, 44 sites (2003: 1, 2, 3, 10, 11, 12, 15, 17, 25, 28, 34; 2006: 462, 469, 481, 483, 491, 501, 517, 522, 528, 531, 538, 539, 550, 552, 563, 564–565, 569, 573, 579; 2014: 209, 215, 222, 234, 239, 246, 252, 256, 260, 277, 299, 305, 311, 319). MM, three sites (121, 122, 123).

In the past, the name *O. haematodus* was applied to what we now know to be several distinct species. Brown (1976) considered *O. haematodus* to be a strictly South American species. More recently, however, exotic populations of true *O. haematodus* have become established in North America (MacGown et al., 2014).

*Odontomachus* workers are large and in most species forage alone as they actively hunt for insect prey. *Odontomachus bauri* is a widespread New World species, known from South America, Central America, and the West Indies (Brown, 1976). This large black trap-jaw ant is common in intact forest habitats on many West Indian islands. Emery (1892) described *O. bauri*, but later Emery (1911) designated this a subspecies of *O. haematodus*. Taylor and Wilson (1962) revived its status as a full species. Brown (1976) notes that the species group that *O. bauri* belongs to is “represented by a number of species so closely related, and at the same time so variable, that they have defied analysis for more than a century.” The West Indian *Odontomachus* species have numerous unresolved taxonomic problems (Brown, 1976; Lubertazzi, 2019). This includes problems with determining what names to apply to the West Indian *Odontomachus* and how many species occur in the region.

**\*32. *Odontomachus ruginodis* Smith**

*Published Records.* No site data (HS; Forel, 1897 as misidentified *O. haematodes insularis*).

*New Specimens.* C&W, three sites (G29, G61, G151). JW, 16 sites (2003: 7, 16, 30, 41; 2006: 494, 497, 537, 539–540, 553–555, 557; 2014: 203, 216, 245, 258, 284, 302). MM, one site (123).

We believe that Forel's (1897) record of this valid species is misidentified *O. ruginodis*, originally described as a variety of *O. insularis*. True *O. insularis* are known from the Greater Antilles and the Bahamas.

*Odontomachus ruginodis* is a widespread New World species that is probably native to the West Indies (Deyrup et al., 1998), but may be exotic in Florida (Deyrup, 1991). Brown (1976) regarded *O. ruginodis* as synonymous with *Odontomachus brunneus*. Brown (in Deyrup et al., 1985), however, changed his mind, and again separated them into two distinct species. This species is often misidentified as *O. insularis*. This species is common in a wide variety of habitats, including highly disturbed urban areas.

**33. *Paratrechina longicornis* (Latreille)**

*Published Records.* No site data (HS; Forel, 1897). Richmond Hill (CB; MCZ; Wheeler, 1911).

*New Specimens.* C&W, two sites (G137, G154). JW, 41 sites (2003: 5, 7, 9, 10, 20, 23, 24, 27, 30, 37, 41; 2006: 494, 497, 504, 534–535, 536, 537, 538, 550, 553, 556, 557, 559, 562, 572; 2014: 205, 215, 256, 267, 269, 272, 273, 278, 279, 280, 282, 283, 285, 289, 302, 305, 307). JE, two sites (F2, F3). MM, one site (119).

The longhorn crazy ant, *Paratrechina longicornis*, is an Old World tramp species spread throughout the tropics and subtropics by human commerce (Wetterer, 2008). This species is simple to recognize because of its extremely long antennae. *Paratrechina longicornis* is a ubiquitous agricultural and

household pest throughout much of the tropics and subtropics and is a pervasive indoor pest in temperate areas. It thrives even in the most artificial environments, including ships at sea, facilitating its dispersal around the world (Wetterer, 2008).

**34. *Pheidole antillana* Forel**

*Published Records.* No site data (HS; Forel, 1897 as *Pheidole guilelmi-mülleri antillana nigrescens*). Grand Etang (CB; Wheeler, 1911). Wilson (2003).

*New Specimens.* C&W, five sites (G1, G19, G24, G38, G75, G83, G85, G94, G96, G122). JW, six sites (2003: 3, 12, 25, 34–36; 2014: 219, 229).

Forel (1893) included these field notes by HS concerning *P. antillana*: “A common species in forest and shady places. The colonies are generally composed of one or two hundred individuals at most, but may have as many as six or seven hundred. The nest is generally under bark of very rotten logs, or under a log or stick; rarely under a stone or under turf on a rock. It is an irregular chamber, with short radiating passages, the whole commonly occupying only two or three inches of space. The workers major are few in number, sometimes only one or two in the colony. Both workers major and minor are sluggish, especially the former.”

**35. *Pheidole bruesi* Wheeler**

*Published Records.* Grand Etang (CB; Wheeler, 1911; MCZ). Wilson (2003).

*New Specimens.* C&W, four sites (G50, G54, G80, G90, G140, G157). JW, two sites (2003: 25; 2014: 309).

Wheeler (1911) described this species as *Pheidole triconstricta bruesi*, which seems to explain why Antweb and AntWiki list *Pheidole triconstricta*, a species otherwise only reported from Bolivia, Brazil, Paraguay, and Uruguay, as also occurring in Grenada. Wilson (2003) wrote: “At La Sagesse Bay, Stefan Cover and I found *P.*

*bruesi* abundant in dry, semi-deciduous scrub woodland, nesting in soil covered by thin leaf litter. At Fort Jeudy, a nest was found in dry deciduous forest, in a small rotting stump with galleries extending downward into the soil. In a nutmeg grove at Concord Falls, we found nests common in the soil. A nest excavated at Sagesse Bay contained a single queen. Majors and minors were readily attracted to baits, following odor trails laid by individually foraging scout workers.”

### 36. *Pheidole flavens* Roger

*Published Records.* No site data (HS; Forel, 1897). Richmond Hill (CB; Wheeler, 1911).

*New Specimens.* C&W, three sites (G7, G39, G41, G44, G147). JW, 22 sites (2003: 2, 12, 15, 40, 25; 2006: 463; 2014: 203, 210, 230, 247, 253, 255, 258, 262–263, 281, 283, 284, 296, 298, 304, 305, 306, 309, 316, 320). MM, one site (123)

Wilson (2003) wrote: “The wide range and abundance of *Pheidole flavens* is due at least in part to its ability to use different microhabitats as nesting sites. Judging from the extensive data of HS (in Forel 1893j) on St. Vincent and J. T. Longino (1997) in Costa Rica, as well as my own collecting records, *flavens* prefers rotting pieces of wood, but also utilizes spaces beneath the bark of trees, dead knots on tree trunks, sod on rocks, the soil beneath stones, and epiphyte masses... The nest galleries are diffuse and irregular, the queens hard to find, and mature colonies large, containing up to thousands of workers.”

Wilson (2003) wrote: “At La Sagasse Bay on Grenada, West Indies, Stefan Cover and I found several colonies of *exigua* in small pieces of rotten wood on the floor of dry semi-deciduous forest. A colony of the closely similar *P. flavens* was in a rotten stump on the grounds of an ecotourism resort several hundred meters away.” Stefan Cover reexamined these specimens and

determined that both colonies were *Pheidole flavens*.

### +37. *Pheidole indica* Mayr

*Published Records.* None.

*New Specimens.* JW, one site (2014: 275).

*Pheidole indica* is an Old World ant species that has spread to other parts of the world through human commerce. Almost all West Indian records of *P. indica* (as its junior synonym *P. teneriffana* Forel) come from beaches or urban areas (Wetterer, 2011a). Although similar in size and coloration as its highly destructive congener, the African big-headed ant, *Pheidole megacephala* (Fabricius), it seems doubtful that *P. indica* will develop into a similarly important pest species.

### 38. *Pheidole jelskii* Mayr

*Published Records.* No site data (HS; Forel, 1897 misidentified as *Pheidole fallax*). Grand Etang (CB; Wheeler, 1911). Sauteurs (CB; Wheeler, 1911).

*New Specimens.* C&W, two sites (G62, G64, G92). JW, 30 sites (2003: 7, 9, 10, 16, 24, 27, 30, 36, 41; 2006: 462, 463, 466, 481, 490, 494–496, 497, 505, 518–519, 522, 536, 538, 540, 564, 569, 572, 573; 2014: 221, 243, 266, 276). MM, two sites (123, 125).

*Pheidole jelskii* is a widespread New World species known from South America and the West Indies (Wilson, 2003). This large species is common in Grenada, with conspicuous ground nests in open sunny areas. Wilson (2003) wrote: “*P. jelskii* is a species that nests in bare soil and open spaces. As such it is well adapted to disturbed habitats of all kinds, from cultivated fields to pastures to roadsides, as well as marginal natural environments such as beaches and river banks. In many places it is extremely abundant, although colony densities vary locally... They typically construct conspicuous crater nests with slit-shaped entrances in open soil, but also less regular nests with irregular entrances in vertical



banks of soil in heavily disturbed locations. The minors forage singly over distances of up to ten meters or more, and are extremely swift and efficient at laying odor trails over even very loose soil to recruit other minors as well as majors to dead insects and sugar baits. The majors release a strong fetid odor, possibly from skatole, when the colonies are disturbed.” Forel’s (1897) record of *P. fallax* from Grenada was based on misidentified *P. jelskii*. Wilson (2003) wrote of *P. fallax*, “no certain records exist from the Lesser Antilles, where the closely related *jelskii* abounds.”

### 39. *Pheidole sculptior* Forel

*Published Records.* (HS; Forel, 1897 as *Pheidole flavens sculptior grenadensis*.) Wilson (2003).

*New Specimens.* C&W, three sites (G51, G55, G124, G150). JW, 29 sites (2003: 3–4, 17, 28, 30, 36; 2006: 462, 464, 481, 485, 490, 492, 500, 501, 506, 517, 522, 539–541, 548, 550, 552, 553, 564, 578, 579; 2014: 219, 248, 254, 279, 290, 313).

*Pheidole sculptior* is widespread in the West Indies and northern South America (Wilson, 2003). It is common in a wide range of habitats in Grenada. Wilson (2003) wrote: “On St. Vincent in the early 1890s, the avid collector H. H. Smith (in Forel 1893j) found *sculptior* to be relatively scarce but very adaptable in habitat. Ranging from sea level to 500 m, it occurred in forests, seashore thickets, and open land. Nests were in loamy soil under pieces of dead wood or stones; one was found in a piece of rotten wood. The colonies were small, in one instance noted by Smith comprising about 200 workers.”

### +40. *Pheidole subarmata* Mayr

*Published Records.* Wilson (2003).

*New Specimens.* C&W, four sites (G36, G43, G68, G136). JW, four sites (2006: 497, 553; 2014: 269, 297, 310). MM, one site (123).

*Pheidole subarmata* is a widespread New World species known from South America, Central America, and the West Indies, common in disturbed habitats (Wilson, 2003). Wilson (2003) wrote: “*Pheidole subarmata* favors moist soil in open places, including habitats seriously disturbed by human activity—such as the edges of dirt roads, agricultural fields, coconut groves, secondary rainforest, city parks, and seashores. When exploring in the deeper rainforest is done, it is usually easy for the collector to add *subarmata* to his list by searching adjacent roads and fields.”

### +41. *Plagiolepis alluaudi* Emery

*Published Records.* Wetterer (2014a).

*New Specimens.* C&W, one site (G17). JW, one site (2003: 15).

This small yellow-orange ant is a tramp species that has been spread around the world through human commerce (Wetterer, 2014a). *Plagiolepis alluaudi* is a primarily tropical species, apparently native to Madagascar and neighboring islands. It has become a pest on Pacific islands and in European greenhouses. Recent records of *P. alluaudi* from nine tropical islands in the West Indies indicate a substantial New World invasion (Wetterer, 2014a).

### 42. *Platythyrea punctata* (Smith)

*Published Records.* No site data (HS; Forel, 1897 as *Platythyrea pruinosa*). Grand Etang (CB; Wheeler, 1911). Richmond Hill (CB; Wheeler, 1911).

*New Specimens.* C&W, two sites (G4, G22, G67). JW, nine sites (2003: 12; 2006: 466, 485, 517, 522, 577; 2014: 219, 232, 260).

*Platythyrea punctata* is a circum-Caribbean species found in a wide range of habitats (Brown, 1975). Seal *et al.* (2011) made genetic analyses of *P. punctata* specimens from a wide range of sites in the West Indies, Central America, Mexico, Texas, and Florida. Seal *et al.* (2011)

estimated that *P. punctata* spread from Central America and through the West Indies about 150,000 years ago (kya). *Platythyrea punctata* inhabits wooded areas where we often encountered solitary foragers scurrying on open ground within forests, e.g., crossing forest trails.

**+43. *Prionopelta antillana* Forel**

*Published Records.* None.

*New Specimens.* C&W, one site (G118). JW, two sites (2014: 311, 320).

Forel (1909) described *Prionopelta antillana* from St. Vincent. In addition to records from the Lesser Antilles, this tiny yellow species has records from wide-ranging locales in Central and South America, plus exotic records from Florida and possibly Cuba. Although it was once thought that *P. antillana* may be introduced to the Lesser Antilles (Brown, 1960), *P. antillana* is now known from most major islands of the Lesser Antilles north to St. Kitts (17.4°N), a pattern that is consistent with natural spread through relatively short-distance island-hopping from South America and Trinidad. The only record of *P. antillana* from the Greater Antilles, a single report from Cuba lacking collection information, is distant from any continental population source and may be introduced. Little is known about the ecology of this ant and no males have been described (Deyrup et al., 2000).

**44. *Pseudomyrmex* sp. PSW-52**

*Published Records.* No site data (Ward, 1992).

*New Specimens.* C&W, two sites (G21, G116, G117). JW, three sites (2006: 485, 490; 2014: 250).

Ward (1992) listed the arboreal twig ant species *Pseudomyrmex* sp. PSW-52 from Grenada as well as southern Central America and northern South America. Philip Ward is currently working on taxonomic analysis of this species.

**45. *Pseudoponera stigma* (Fabricius)**

*Published Records.* Grand Etang (CB; Wheeler, 1911).

*New Specimens.* C&W, three sites (G119, G141, G146, G149). JW, five sites (2003: 38; 2006: 522; 2014: 277, 319, 320).

*Pseudoponera stigma* is an inconspicuous forest species that generally nests in and under rotten logs and feeds on termites. This species has an extensive range in both the New World and Old World tropics, but there has been disagreement on where *P. stigma* is native. Wetterer (2012b) concluded that the weight of evidence indicates that *P. stigma* originated in tropical South and Central America.

**+46. *Rogeria curvipubens* Emery**

*Published Records.* None.

*New Specimens.* JW, six sites (2003: 10; 2006: 466, 501; 2014: 210, 242, 306).

*Rogeria curvipubens* is a widespread New World species known from northern South America, Central America, and the West Indies (Kugler, 1994; LaPolla and Sosa-Calvo, 2006).

**+47. *Rogeria foreli* Emery**

*Published Records.* None.

*New Specimens.* C&W, one site (G143). JW, 24 sites (2003: 10, 34; 2006: 462, 466, 468, 481, 494, 501, 506, 517, 540, 548; 2014: 210, 213, 239, 242, 260, 281, 283, 284, 289, 302, 309, 311).

*Rogeria foreli* is a widespread New World species known from northern South America, Central America, the West Indies, and the southwestern U.S. (Kugler, 1994; LaPolla and Sosa-Calvo, 2006). We found this species in a variety of habitats in Grenada.

**48.–55. *Solenopsis* spp.**

*Unidentified Specimens.* C&W, two sites (G69, G100, G128, G132). JW, 15 sites (2014: 208, 209, 219, 230, 242, 250, 260, 267, 284, 288, 296, 309, 311, 317, 320).

The genus *Solenopsis* is often informally divided into two groups: “fire ants” and “thief ants.” Fire ants are relatively large, polymorphic, and with a potent sting (e.g., *S. geminata* and *S. invicta*). Thief ants are usually small, monomorphic, and not known to sting humans. *Solenopsis globularia* falls between these two categories; it is intermediate in size, polymorphic, and not known to sting humans.

Fire ants include some major pest species, including the tropical fire ant *S. geminata*. Thief ants are generally overlooked because of their small size and primarily subterranean habits. Thief ants commonly persist at high densities in areas invaded by dominant exotic ants such as *Pheidole megacephala* and *Linepithema humile* (Wetterer and Wetterer, 2004). Thief ants are most often collected in extractions of leaf litter samples and little is known about the ecology of different species. Despite previous work on the taxonomy of thief ants (Pacheco and Mackay, 2013), much taxonomic work remains to be done on this challenging group.

Pacheco and Mackay identified the *Solenopsis* thief ants JW collected in 2003 and 2006. Concerning different species of thief ants, Pacheco and Mackay (2013) wrote: “Workers are very difficult to identify without females. For example, workers of *Solenopsis castor*, *S. conjurata*, *S. corticalis*, *S. gnoma*, *S. nickersoni*, *S. picta*, *S. subtilis*, *S. sulforea*, *S. tenuis*, and *S. zeteki* are nearly identical. Likewise the workers of *S. basalis*, *S. clytemnestra*, *S. decipiens*, *S. franki*, *S. helena*, *S. joergenseni*, *S. laeviceps*, *S. latastei*, *S. loreтана*, *S. major*, *S. molesta*, *S. parva*, *S. picea*, *S. quadridentata*, *S. rosella*, *S. salina*, *S. striata*, and *S. validiuscula* are difficult to separate. Workers of a third group, consisting of *S. abdita*, *S. abjector*, *S. carolinensis*, *S. maboaya*, *S. orestes*, *S. patriciae*, *S. pollux*, and *S. texana*, are nearly impossible to separate.” We have left thief ant specimens from the 1995 and 2014 collections as identified only to genus,

except for *Solenopsis globularia*, which is very distinctive.

#### +48. *Solenopsis azteca* Forel

*Published Records.* Pacheco and Mackay (2013).

*New Specimens.* JW, eight sites (2003: 2, 25, 34, 35–36, 40, 2006: 463–464, 468, 579).

This tiny thief ant has monomorphic workers that range in color from light yellow to light brown (Pacheco and Mackay, 2013). *Solenopsis azteca* is a New World species with a known range of “Honduras south to Colombia (Cauca) and northern Venezuela, Caribbean Region (Jamaica, Puerto Rico, Antilles)” (Pacheco and Mackay, 2013).

#### 49. *Solenopsis castor* Forel

*Published Records.* No site data (HS; Forel, 1897). Pacheco and Mackay (2013).

*New Specimens.* JW, one site (2006: 550).

This tiny yellow thief ant has been recorded from “Mexico (Colima) south to Panama (Chiriqui), Caribbean (Antilles St. Vincent, Grenada, Dominica) and Bolivia” (Pacheco and Mackay, 2013).

#### 50. *Solenopsis geminata* (Fabricius)

*Published Records.* No site data (HS; Forel, 1897). Richmond Hill (CB; Wheeler, 1911).

*Unpublished Records.* Greenville (1941; EMcC Callen; USNM). 1 mi E Grand Roydothan (DH Kistner; AntWeb FMNHINS0000121831).

*New Specimens.* C&W, two sites (G34, G156). JW, 74 sites (2003: 1, 5, 6, 7, 8, 9, 10, 11, 12, 14, 16, 17, 19, 20, 23, 24, 29, 37, 41; 2006: 462, 463, 466, 468, 481, 490, 494, 497, 500, 505, 507, 517, 522, 531, 536, 537, 538, 539–540, 548–549, 550, 552, 553, 557, 562, 563, 564, 569, 571, 572, 574; 2014: 208, 212, 213, 215, 217, 218, 227, 241, 256, 258, 266, 268, 271, 272, 273, 278, 281, 283, 284, 288, 289, 302, 305, 306, 308). JE, one site (F5). MM, four sites (119, 120, 121, 123).

The tropical fire ant, *Solenopsis geminata*, is native to the New World, where in disturbed areas, it can reach very high densities and dominate the invertebrate community (Risch and Carroll, 1982). It is also an invasive pest in many other parts of the world, including many tropical and subtropical areas where sea turtles nest, such as Australia, islands of the Pacific and Indian Oceans, the Arabian Peninsula, India, South Africa, Greece, and Cyprus (Wetterer, 2011b). *Solenopsis geminata* nests are marked by piles of soil around their nest entrances that may be built up around a stump, downed wood, or grass. Unlike the other *Solenopsis* species on Grenada, which all have very small workers, *S. geminata* workers are larger and continuously polymorphic. Their nests are often found at the edge of open areas; they do not inhabit areas with dense shade. Foragers often recruit large numbers of workers when food is discovered and workers can be aggressive when disturbed (Creighton, 1930; Trager, 1991)

### 51. *Solenopsis globularia* (Smith)

*Published Records.* No site data (HS; Forel, 1897). Pacheco and Mackay (2013).

*New Specimens.* C&W, two sites (G66, G139). JW, 20 sites (2003: 7, 10, 29; 2006: 468, 497, 505, 531, 536, 537, 550, 562, 572; 2014: 203, 208, 215, 258, 278, 281, 283, 284, 305).

*Solenopsis globularia* is a widespread New World species that ranges from Corrientes, Argentina (28.4°S) in the south to Craven County, North Carolina (35.1°N) in the north (Pacheco and Mackay, 2013) and throughout the West Indies. It also occurs on the Atlantic islands of Ascension, St. Helena, and Cabo Verde (Wetterer et al., 2007; Wetterer, in press), and has recently been reported from Ivory Coast (Kouakou et al., 2018). Unlike smaller thief ants, workers of this species can be found foraging in exposed situa-

tions, and will actively recruit workers to baits.

### +52. *Solenopsis maboya* Snelling

*Published Records.* None.

*New Specimens.* JW, one site (2006: 466).

*Solenopsis maboya* is otherwise only known from Puerto Rico. Although Pacheco and Mackay (2013) did not include this record of *S. maboya* from Grenada in their paper, J. Mackay and W. Pacheco made this specimen identification. Pacheco and Mackay (2013) wrote “The workers of *Solenopsis maboya* are most similar to *S. corticalis*.” Because *S. corticalis* has widespread records from Central and South America and the West Indies, including St. Vincent (Pacheco and Mackay 2013), it seems more likely that this record is misidentified *S. corticalis*.

### +53. *Solenopsis pollux* Forel

*Published Records.* Pacheco and Mackay (2013).

*New Specimens.* JW, nine sites (2003: 3–4, 11, 25, 38. 2006: 462, 463, 517, 522, 548).

*Solenopsis pollux* is a widespread New World species known from South America, Central America, and the West Indies in a wide range of habitats (Pacheco and Mackay, 2013). Concerning this tiny thief ant, Pacheco and Mackay (2013) wrote: “Care must be taken in the Caribbean region where *S. pollux* and *S. corticalis* are common, as confusion could result between them, especially on the island of St. Vincent.”

### +54. *Solenopsis pygmaea* Forel

*Published Records.* Pacheco and Mackay (2013).

*New Specimens.* JW, two sites (2006: 501, 528).

*Solenopsis pygmaea* is a widespread New World species known from Central America and the West Indies (Pacheco and Mackay, 2013).



**+55. *Solenopsis zeteki* Wheeler***Published Records.* None.*New Specimens.* JW, one site (2006: 463).

*Solenopsis zeteki* is a widespread New World species known from northern South America, Central America, and the West Indies (Pacheco and Mackay, 2013). Although this record was not included in Pacheco and Mackay (2013), Mackay and Pacheco made this identification.

**56.–64. *Strumigenys* spp.** *Strumigenys* ants (Hymenoptera, Formicidae) are small predatory ants that generally feed on springtails (Collembola) and other tiny arthropods (Wilson, 1954). *Strumigenys* spp. are slow moving, rarely forage openly above ground, and typically become motionless when disturbed. Most people, including field biologists, remain unaware of their presence even in areas where they are common.

**56. *Strumigenys alberti* Forel***Published Records.* Balthasar (HS; Bolton, 2000).*New Specimens.* JW, one site (2014: 316).

Forel (1893) described *S. alberti* from St. Vincent. It has been reported from many sites in Central America, South America, and the West Indies (Bolton, 2000).

**+57. *Strumigenys eggersi* Emery***Published Records.* Wetterer (2018).*New Specimens.* JW, seven sites (2003: 35; 2006: 506, 528; 2014: 210, 250, 311, 320).

*Strumigenys eggersi* is a widespread New World species (Bolton, 2000). Brown (1959) proposed that this species' "home range is probably south Brazil and Bolivia, though a lack of collections from central and northern Brazil prevents us from knowing how far north this species extends. *S. eggersi* is also known from widely scattered localities in the West Indies, Florida, and southern Mexico ... and it seems likely that it has been

introduced by man at these many points." Brown (1962), however, seemed more unsure of the species exotic range, writing that *S. eggersi* was "widespread (possibly by recent introduction) in the West Indies; southern Florida; southern Mexico."

**+58. *Strumigenys elongata* Roger***Published Records.* None.*New Specimens.* JW, three sites (2006: 501; 2014: 210, 311).

There are widespread records of this species in Central and South America (Bolton, 2000). In the Lesser Antilles, *S. elongata* is known from Trinidad, Grenada, St. Vincent, and Guadeloupe.

**+59. *Strumigenys emmae* (Emery)***Published Records.* Wetterer (2012b).*New Specimens.* JW, four sites (2006: 501, 540, 562; 2014: 242).

*Strumigenys emmae* has spread to many parts of the world through human commerce (Wetterer, 2012c). *Strumigenys emmae* appears to be originally from the Australian region, where all its closest relatives are found. *Strumigenys emmae* occurs primarily in tropical areas. Almost all subtropical records come from peninsular Florida, plus a few subtropical records from the Bahamas, Japan, and Australia. *Strumigenys emmae* is most commonly found in intact xeric and mesic forest, as well as in planted areas around buildings, but rarely occurs in moist habitats. *Strumigenys emmae* is one of three Old World dacetine ants, along with *Strumigenys membranifera* and *Strumigenys rogeri*, with widespread records in both the Old World and the New World.

**+60. *Strumigenys margaritae* (Forel)***Published Records.* MacGown and Wetterer (2013).*New Specimens.* JW, 23 sites (2003: 11, 12, 25, 39; 2006: 462, 468, 490, 497, 501, 504, 517, 522, 539, 540, 564, 579; 2014: 211, 213, 227, 239, 260, 311, 316).

*Strumigenys margaritae* is a widespread New World species (MacGown and Wetterer, 2013). Although rare in many parts of its range, *S. margaritae* appears to have an essentially continuous circum-Caribbean distribution from northern South America to the southeastern U.S. and through the Lesser Antilles from Trinidad to Puerto Rico. If this distribution is truly continuous, it would support the hypothesis that *S. margaritae*, though often considered exotic to the southeastern U.S., is actually native throughout its known range.

*Strumigenys margaritae* is commonly found associated with *Wasmannia auropunctata*, an aggressive and often dominant Neotropical species. *Strumigenys margaritae* may derive protection from predators by associating with *W. auropunctata*. It is also possible that *S. margaritae* might afford some benefit to *W. auropunctata*.

*Strumigenys margaritae* is common in a wide range of habitats in Grenada.

#### +61. *Strumigenys rogeri* Emery

*Published Records.* Wetterer (2012a).

*New Specimens.* JW, five sites (2006: 517; 2014: 208, 242, 296, 311).

*Strumigenys rogeri* apparently originated in tropical Africa, where all its closest relatives live, but it has become widespread on tropical islands of the Indo-Pacific and the West Indies, and in peninsular Florida (Wetterer, 2012a). Outside of Africa and Florida, there are only a small number of continental records of *S. rogeri*, including a few from South and Central America and just one from continental Asia, in peninsular Malaysia. It is unclear whether *S. rogeri* has not yet spread to these continental areas, whether continental ants have competitively excluded *S. rogeri*, or whether these ants have been simply overlooked in surveys of diverse continental faunas.

#### +62. *Strumigenys silvestrii* Emery

*Published Records.* None.

*New Specimens.* JW, one site (2006: 540).

Throughout its New World range (South America, the West Indies, and the southern U.S.), most *S. silvestrii* records come from intact forest (MacGown et al., 2012). The distribution of its closest relatives and of known *S. silvestrii* specimen records supports the hypothesis that *S. silvestrii* is native to South America. *Strumigenys silvestrii* has been found for the first time in the Old World, from the island of Madeira, mainland Portugal, and Macau (MacGown et al., 2012).

#### 63. *Strumigenys smithii* Forel

*Published Records.* No site data (HS; Forel, 1897). Black Forest Estate (HS; Bolton, 2000).

*New Specimens.* C&W, one site (G120). JW, nine sites (2003: 2, 25, 34–35, 38; 2006: 485, 517, 522, 573; 2014: 316).

This species, the largest *Strumigenys* of Grenada, is known from scattered sites across Central and South America and a few West Indian islands (Bolton, 2000). It is most commonly found nesting in rotten logs in forest areas.

#### +64. *Strumigenys subedentata* (Mayr)

*Published Records.* None.

*New Specimens.* C&W, one site (G79, G87, G93).

This forest species is widespread in Central and South America (Bolton, 2000). It is known in the West Indies from Trinidad and Guadeloupe.

#### +65. *Sylophopsis sechellensis* (Emery)

*Published Records.* Wetterer and Sharaf (2017).

*New Specimens.* JW, two sites (2003: 30; 2006: 552)

*Sylophopsis sechellensis* (formerly *Mono-morium sechellense*) is a tramp ant species that has spread by human commerce to many Old World sites. The geographic ranges of *S. sechellensis* and other *Sylo-*

*phopsis* species suggest that *S. sechellensis* may be native to Madagascar and neighboring islands in the western Indian Ocean or to Southeast Asia. Wetterer and Sharaf (2017) documented records of *S. sechellensis* in the New World from 12 West Indian islands.

**+66. *Syllophopsis subcoeca* (Emery)**

*Published Records.* None.

*New Specimens.* JW, three sites (2014: 208, 215, 284).

*Syllophopsis subcoeca* (formerly *Mono-morium subcoecum*) is largely subterranean and is usually found through sifting. This species is similar in appearance to *S. sechellensis*, but they may be distinguished by this character: the mesopleuron is shiny and unsculptured in *subcoeca*, whereas it is matte and microreticulate in *sechellensis*.

Although all previously published records of *S. subcoeca* come from the New World, Torres and Snelling (1997) considered it to be an Old World native, as are all other known members of the genus. Wetterer et al. (2016) provisionally classified *S. subcoeca* as a New World species. In addition to specimens from Grenada, Mostafa Sharaf identified numerous specimens of *S. subcoeca* that JW collected on other West Indian islands, including Barbados, Dominica, Guadeloupe, Martinique, Nevis, St. John, St. Kitts, St. Lucia, Tortola, and Trinidad. Sharaf, however, also identified *S. subcoeca* that JW collected in Singapore and that Orty Bourquin collected in the Northern Mariana Islands, lending weight to the proposition that *S. subcoeca* is an Old World species. Genetic studies should evaluate Old and New World specimens of *S. subcoeca* to determine where this species is native.

**+67. *Tapinoma melanocephalum* (Fabricius)**

*Published Records.* Wetterer (2009a).

*New Specimens.* C&W, one site (G42). JW, 28 sites (2003: 5, 9, 16, 24; 2006: 494, 497, 500, 505, 532, 538, 539–540, 550, 552, 557–558, 562, 563, 572, 578; 2014: 239, 256, 258, 260, 267, 279, 284, 302, 306, 310). MM, one site (120).

The ghost ant, *T. melanocephalum*, is a ubiquitous indoor and outdoor pest throughout much of the tropics and subtropics, and a common indoor pest in temperate regions (Wetterer, 2009a). This species is easily identified by its distinctive coloration, dark head and mesosoma and pale gaster. The close resemblance between *T. melanocephalum* and several Indo-Pacific taxa indicates that *T. melanocephalum* probably originated in this region. *Tapinoma melanocephalum* has one of the widest distributions known for any ant species. It has spread across the Old World and New World in both the Northern and Southern hemispheres, though at latitudes greater than 30° it is largely restricted to living inside buildings.

**68. *Tetramorium bicarinatum* (Nylander)**

*Published Records.* Wetterer (2009b).

*New Specimens.* Saint George's, Botanical Gardens, (1918; H Morrison; USNM). C&W, two sites (G25, G138). JW, one site (2003: 20).

*Tetramorium bicarinatum*, formerly misclassified as *Tetramorium guineense* (Fabricius), has long been recognized as one of the world's most broadly distributed ant species. *Tetramorium bicarinatum* is widespread throughout much of the tropics and subtropics by human commerce, except for continental Africa and West Asia, where it is largely absent (Wetterer, 2009b). In addition, *T. bicarinatum* is found in temperate areas inside greenhouses and heated buildings. Analysis of its known distribution and those of its closest relatives strongly suggests that *T. bicarinatum* originated in the Indo-Pacific. *Tetramorium bicarinatum* is occasionally reported as an agricultural pest

because of its habit of tending phloem-feeding Hemiptera.

**+69. *Tetramorium simillimum* (Smith)**

*Published Records.* None.

*New Specimens.* C&W, one site (G27, G33). JW, 14 sites (2003: 16; 2006: 497, 552; 2014: 203, 242, 267, 269, 273, 278, 279, 283, 284, 296, 302).

Bolton (1979) wrote that *T. simillimum* “has been widely recorded throughout the tropics and subtropics and also occurs fairly frequently in the temperate zones in zoological and botanical gardens and in conservatories and other constantly heated buildings.” We found this species at many highly disturbed sites in Grenada.

**+70. *Trichomyrmex destructor* (Jerdon)**

*Published Records.* Wetterer (2009c).

*New Specimens.* JW, 21 sites (2003: 1, 4, 8, 9, 16, 23, 37, 41; 2006: 494, 497–498, 505, 531, 538, 551, 552, 572; 2014: 203, 270, 279, 283, 288). JE, one site (F4). MM, one site (120).

The destroyer ant, *T. destructor* (formerly *Monomorium destructor*), is a pest in many tropical and subtropical areas, where it is notorious for chewing through the insulation of electrical wires, living in and destroying electrical equipment, and attacking people (Wetterer, 2009c). *Trichomyrmex destructor* most closely resembles several African species, and has a seemingly continuous distribution from North Africa to Southeast Asia, suggesting that *T. destructor* originated in North Africa, but is also native to the Middle East and South Asia. *Trichomyrmex destructor* is most common as a pest in disturbed arid and semiarid habitats in the tropics and subtropics. Outbreaks of *T. destructor* often appear to be localized and short-lived. This pattern of population explosion followed by decline should be taken into consideration in any large-scale efforts to control these ants.

**71. *Wasmannia auropunctata* (Roger)**

*Published Records.* Grand Etang; 1900ft (HS; BMNH; Forel, 1897). Balthazar (HS; BMNH; Forel, 1897). Richmond Hill (CB; MCZ; Wheeler, 1911). Sauteurs (CB; Wheeler, 1911).

*New Specimens.* C&W, two sites (G53, G127). JW, 74 sites (2003: 2, 3–4, 9, 10, 12–13, 15, 40, 17, 20, 23, 24, 26, 27, 28, 29, 34, 36, 38, 39; 2006: 462, 463, 465, 468, 481, 482, 485, 490, 494, 497, 500, 501, 506, 507, 517, 522, 531, 536, 537, 538, 539–540, 548, 550, 552, 553, 562, 563, 564, 569, 572, 573, 575–576, 579; 2014: 208, 209, 213, 220, 227, 239, 240, 251, 258, 261, 267, 272, 283, 289, 296, 305, 306, 309, 310, 312, 318, 322). MM, two sites (121, 122).

The little fire ant, *W. auropunctata*, occurs throughout most of the warmer parts of the New World, from subtropical Argentina to subtropical Mexico and through much of the West Indies, though it is not clear whether this species is native to this entire region. In many areas, *W. auropunctata* can be a significant agricultural pest, not only stinging agricultural workers, but also enhancing populations of Hemiptera. Hemiptera cause damage both through sapping plants of nutrients and by increasing the occurrence of diseases, including viral and fungal infections. In addition, *W. auropunctata* has a negative impact on many animals, both invertebrates and vertebrates, though most reports on such impact have been anecdotal. Reports of widespread blindness in both domestic and native mammals caused by *W. auropunctata* stings deserve serious attention (Wetterer, 2013a).

**Species with No Recent Records**

Earlier collectors, notably HS and CB, found several ant species in Grenada that have never been collected again. These species may be variously misidentified, overlooked, or extinct in Grenada.



**72. *Cephalotes pallens* (Klug)**

*Published Records.* No site data (HS; Forel, 1897 as *Cryptocerus araneolus*).

De Andrade and Baroni Urbani (1999) wrote, “Forel (1897) reports “*Cryptocerus araneolus*” from Grenada (Lesser Antilles) and, presumably on this sole basis, Kempf (1972) listed Grenada under the geographic distribution of *pallens*. We did not find specimens from Grenada either in the Forel collection or in other collections. Kempf’s deduction, hence, remains probable but worthy of confirmation because of the set of new species similar to *pallens* described in this paper.”

This is a widespread species of “turtle ant” that nests in hollow vegetation. Future studies should look for this species nesting in red mangroves, a habitat where *Cephalotes* species are relatively common.

**73. *Crematogaster laevis bruesi* Wheeler**

*Published Records.* Grand Etang (CB; Wheeler, 1911; MCZ).

The only record of this taxon is from the Grenada type series (Wheeler, 1911). The typical *Crematogaster laevis* is known from South America.

**74. *Leptogenys arcuata* Roger**

*Published Records.* No site data (HS; Forel, 1897).

This species is known from South America and some West Indian islands, including St. Vincent and Guadeloupe (Lattke, 2011). Lattke (2011), however, wrote that *Leptogenys arcuata*: “can be confused with members of the more commonly encountered *L. pubiceps* complex.”

**75. *Leptogenys pubiceps* Emery s.l.**

*Published Records.* Grand Etang (CB; Wheeler, 1911 as *Leptogenys punctaticeps*; MCZ; det. J.E. Lattke; Lattke, 2011 as *L. pubiceps* complex)

We assume the three Brues specimens in the MCZ that Lattke (2011) identified as *L.*

*pubiceps* complex are the same specimens that Wheeler (1911) identified as *L. punctaticeps*. This is the only *Leptogenys* species from Grenada whose specimens Lattke (2011) examined. It is possible that Forel’s (1897) *L. arcuata* and Wheeler’s (1911) *L. punctaticeps* were the same species. *Leptogenys pubiceps* is also known from Venezuela (Lattke 2011).

**76. *Nesomyrmex clavipilis* Wheeler**

*Published Records.* Balthazar (HS; Wheeler, 1910a).

Wheeler (1910a) described this species on the basis of a single winged queen in the USNM that HS collected in Grenada. There are no other records of this genus from Grenada.

**77. *Pachycondyla harpax* (Fabricius)**

*Published Records.* Grand Etang (1912–1913; R. Thaxter, MCZ; Mackay and Mackay, 2010; Wetterer, 2016).

The known continental range of *P. harpax* appears to be essentially continuous, extending from Rio Grande do Sul, Brazil in the south (31.8°S) to Wood County, Texas in the north (32.8°N), including the continental islands of Margarita, Tobago, and Trinidad. Isolated island populations of *P. harpax* known from Grenada, Guadeloupe, and Jamaica may be exotic, introduced through human commerce (Wetterer, 2016).

**78. *Pseudomyrmex flavidulus* (Smith)/  
*Pseudomyrmex* PSW-05**

*Published Records.* No site data (HS; Forel, 1897).

This yellow-to-brown twig ant is known from South and Central America and several West Indian islands (Ward, 1992). Philip Ward (personal communication), however, wrote: “The Bahamas and Puerto Rico records are misidentifications. The other records (V, g, T) [St Vincent, Grenada, Trinidad] are what I would call *Pseudo-*

*myrmex* sp. PSW-05 (which may be the same as *P. flavidulus*. This is a gnarly taxonomic complex.)”

#### 79. *Pseudomyrmex simplex* (Smith)

*Published Records.* No site data (Ward, 1992).

This small, yellow twig ant is extremely widespread in Central and South America, the West Indies, including Grenada, as well as in Florida (Kempf, 1972; Ward, 1992).

#### 80. *Pseudomyrmex termitarius* (Smith)

*Published Records.* No site data (Kempf, 1960; Ward, 1992).

This bicolor twig ant has a dark brown head, gaster, and legs, and a light brown thorax and petiole. It is known from Central and South America and from Trinidad, St. Vincent, and Grenada in the West Indies (Kempf, 1960; Ward, 1992).

#### 81. *Thaumatomyrmex* sp.3

*Published Record.* No site data (HS; Jahyny et al., 2015).

A single specimen in BMNH (CASENT0102935) that HS collected in the Mount Gay Estate, Grenada was identified (by an uncredited identifier) as *Thaumatomyrmex cochlearis* Creighton, a species otherwise known only from Cuba. Photographs of this specimen indicate that the head and thorax are much smoother and shinier than those of true *T. cochlearis*. Jahyny et al. (2015) identified this specimen as *Thaumatomyrmex* sp.3, an undescribed species in the *T. ferox* group, also known from Brazil and French Guiana. *Thaumatomyrmex* species are known to use their giant pitchfork-like mandibles for capturing millipedes (Brandão et al., 1991).

#### 82. *Wasmannia sigmoidea* Mayr

*Published Records.* No site data (HS; Forel, 1897).

This rarely reported species is known from Central and South America, with West

Indian records from St. Vincent, Grenada, and Puerto Rico (Longino and Fernández, 2007).

### DISCUSSION

We documented records of 82 ant taxa from island of Grenada (Tables 1–3). Taxonomic uncertainties and incomplete sampling limit the conclusion we can make concerning the biogeography of the ants of Grenada, so our analyses are necessarily preliminary.

The main island of Grenada is only 74% the size of Barbados, yet we found more native New World ant species on Grenada compared with Barbados (65 vs. 46). This may be due to several possible reasons including: 1) Grenada is closer to other landmasses than is Barbados (Fig. 1), 2) during low sea levels 25–15 kya, Grenada was part of a much larger island about 10 times Grenada’s current size (Fig. 1), 3) Grenada is more mountainous than Barbados, and 4) Grenada has more remaining forest cover than Barbados (50.0% vs. 14.7%; indexmundi.com). Conversely, we found fewer exotic Old World ant species on Grenada than on Barbados (17 vs. 24). This might be attributable to lower levels of human impacts and lower levels of exotic species importation as indicated by: 1) lower human population density (315/km<sup>2</sup> vs. 666/km<sup>2</sup>; worldpopulationreview.com 2018), 2) lower levels of imported lumber products (\$23.6 million/year vs. \$81.6 million/year; latest values; wits.worldbank.org, and 3) lower international tourism levels (135,000 vs. 632,000 international tourism arrivals in 2016; www.statista.com). Preliminary analyses indicate that St. Vincent, a similar-size island north of Grenada (Fig. 1), has more New World ant species and fewer Old World ant species than Grenada, a pattern that also may relate to differences in topography and human impacts (Table 4).

Of the 65 New World ant species known from Grenada, only 34 are also known from

Barbados (Tables 1–2). In contrast, 54 of these species are known from St. Vincent, including the 35 New World ant species we collected most often in Grenada (at six or more sites; Tables 1, 2). This is not surprising, given the Grenadine land bridge that nearly connected Grenada and St. Vincent when ocean levels were lower 15 kya (Fig. 1). Only three ant taxa are known solely from Grenada (*Crematogaster laevis bruesi*, *Nesomyrmex clavipilis*, and *Nylanderia* n. sp.), one other is known just from Grenada and neighboring St. Vincent (*Pheidole bruesi*), and one more in Grenada is known only from the Lesser Antilles (*Pheidole antillana*).

Most ant species found on Grenada have broad Neotropical distributions (Tables 1–3). Of the 60 New World species with records outside the Lesser Antilles, 53 are also known from South America, whereas 46 are also known from the Greater Antilles (Tables 1, 2). Four New World ant species in Grenada are known from the Greater Antilles, but not from South America, and only one of these has been reported from any of the Lesser Antilles north of St. Vincent: *Dorymyrmex antillanus*. Perhaps *D. antillanus* island-hopped from the Greater Antilles. In contrast, nine New World ant species in Grenada are known from South America, but not from the Greater Antilles and seven of these have also been reported from Lesser Antilles north of St. Vincent. This suggests that these species may have originated in South America and island-hopped up the Lesser Antilles, but have not spread as far north as the Greater Antilles.

The three most commonly collected species in Grenada, *W. auropunctata*, *Solenopsis geminata*, and *Cyphomyrmex minutus*, are all New World natives that thrive in highly disturbed environments. The first two species can reach very high densities and become serious pests. The latter species is an inconspicuous ant that is often associated with *W. auropunctata*.

Only three New World ant species in Grenada, *S. geminata*, *W. auropunctata*, and *Hypoponera opaciceps*, are cosmopolitan tramp species, spread worldwide via human commerce (Table 2). Most of the Neotropical ants in Grenada are not known as tramp species, so it seems likely that most Neotropical ants in Grenada are native, descended from populations that arrived naturally, primarily from South America. Some New World species, however, could be exotic to Grenada, and others could have a mix of both native and exotic populations. For example, one possibility is that the light-colored form of *Camponotus sexguttatus* is native to Grenada, but the widespread darker form of *C. sexguttatus* is exotic. One New World ant that is spreading through the West Indies but is not yet known from Grenada is the red imported fire ant (*Solenopsis invicta*), a species native to South America (Wetterer, 2013b).

Records for only four of the 17 Old World exotic ants found in Grenada date to before 1995 (Table 3), so many of these invaders may be recent arrivals. The three most common Old World ants we collected in Grenada are the long-horned crazy ant (*Paratrechina longicornis*), the ghost ant (*Tapinoma melanocephalum*), and the destroyer ant (*Trichomyrmex destructor*). These are all extremely widespread household pests, not generally thought to have great environmental impact. The other Old World ant species known from Grenada are mostly quite inconspicuous, although the penny ant (*Tetramorium bicarinatum*) and the little yellow ant (*Plagiolepis alluaudi*) are occasionally agricultural pests. Major Old World tramp ant species that are known from the West Indies, but have not yet been recorded from Grenada, include the African big-head ant (*Pheidole megacephala*), the pharaoh ant (*Monomorium pharaonis* (L.)), and the difficult white-footed ant (*Technomyrmex difficilis* Forel). *Pheidole megacephala* particularly has been known to greatly affect native ants in areas where it invades

(Wetterer, 2007). For example, Wheeler (1910b) reported the impact of *P. megacephala* on the tiny Puerto Rican island of Culebrita: "I was astonished to find [Culebrita] completely overrun with *Ph. megacephala*. This ant was nesting under every stone and log, from the shifting sand of the sea-beach to the walls of the light-house on the highest point of the island. The most careful search failed to reveal the presence of any other species... It is highly probable that *Ph. megacephala*... had exterminated all the other ants which must have previously inhabited Culebrita." Grenada is one of only a few major West Indian islands where *P. megacephala* is not yet known (Wetterer, 2012f).

Our inventory of known ant records is a first step that can serve as a baseline for future ant research in Grenada. The fact that we collected six species at only one site each suggests that there are still more ant species to be found on Grenada. In addition, there were 12 New World ant species previously reported from Grenada that we did not collect, including 10 not seen for more than 100 years (Table 2). Some species that we did not find may now be extinct on Grenada, but we hold out hope that they persist. Five of these species, *Cephalotes pallens*, *Crematogaster laevis bruesi*, *Pseudomyrmex flavidulus*, *Pseudomyrmex simplex*, and *Pseudomyrmex terminarius*, are arboreal, suggesting that future surveys might do well to do more sampling from up in trees. Surveying ants in the red mangroves (*Rhizophora mangle* L.) of Grenada may be particularly productive. Red mangroves provide a unique arboreal habitat, often completely isolated by water from any terrestrial habitat. Many ant species common in red mangroves of South Florida and West Indian islands are rarely found in any other habitat (Wetterer, 2014a,b, 2017; Wetterer and Guerrero, 2017).

In September 2004, Hurricane Ivan ripped through Grenada with 193 kph (120 mph) sustained winds, killing 39

people and severely damaging 90% of the buildings (WMO, 2005). A large portion of the forest, particularly in Grand Etang National Park, was leveled and many upland villages were completely abandoned. Now the forest, however, is growing back. It remains to be seen whether the native ants will continue to thrive in Grenada or whether exotic ants will come to dominate.

## ACKNOWLEDGMENTS

We thank A. Jeremiah of the Grenada Forestry and National Parks Department for help and hospitality; J. Endeman and M. Mancini for providing specimens they collected in Grenada; M. Wetterer for comments on this manuscript; S. Cover, J. Pacheco, W. Mackay, J. LaPolla, M. Sharaf, and P. Ward for ant identifications; and the National Science Foundation (DEB-0515648), Harvard University, and Florida Atlantic University for financial support.

## APPENDIX

### Collection Site Information

Listed as vial numbers: site (latitude, longitude; date).

Cover and Wilson, 14–21 June 1995 (12 sites):

G1–23: Grand Etang; trail to Mt. Qua Qua (12°5'59.9994"N, 61°42'W; 14 June 1995)

G24–33: La Sagesse Bay, 0.25 mi W of Nature Centre (12°1'26.3994"N, 61°40'26.3994"W; 16 June 1995)

G34–38, G136, G151: La Sagesse Bay, Nature Centre (12°1'26.3994"N, 61°40'12"W; 16, 18, and 20 June 1995)

G39–45 and G61–66: La Sagesse Bay, N of Nature Centre (12°1'47.9994"N, 61°40'12"W; 16 June 1995)

G46–60 and G137–139: La Sagesse Bay, Trail to Marquis Pt. (12°1'19.2"N, 61°40'8.3994"W; 16 and 19 June 1995)

G67–G108: Concord Falls, trail to 2nd falls (12°7'11.9994"N, 61°43'11.9994"W; 17 June 1995)

G109–117 and G135: Grand Etang, 1.3 mi SW visitor centre (12°4'48"N, 61°42'W; 18 June 1995)

G118–134: 3 mi WNW Lower Capitol, on road to Gouyave (12°8'24"N, 61°42'W; 18 June 1995)

G140–148: 1 mi WNW Lower Capitol, on road to Gouyave (12°8'24"N, 61°40'12"W; 19 June 1995)



G149–150: 1.2 mi NW Mt. Home on Mt. Hope Rd; Banana plantation (12°9'N, 61°39'35.9994"W; 19 June 1995)

G152–157: Fort Jeudy (12°N, 61°42'36"W; 21 June 1995)

G158–160: St. George's (12°3'36"N, 61°45'W; 21 June 1995)

#### **Wetterer, 8–12 November 2003 (30 sites)**

1: St. George's, Carenage waterfront (12°3'7.1994"N, 61°45'3.5994"W; 8 November 2003)

2: Grand Etang, lookout trailhead (12°5'13.1994"N, 61°41'56.3994"W; 8 November 2003)

3–4 and 25: Grand Etang, 1 km SW crest (12°4'55.2"N, 61°42'7.1994"W; 8 and 11 November 2003)

5: St. George's, fish market (12°3'10.8"N, 61°45'18"W; 8 November 2003)

6: Prickly Point, scrub (11°59'24"N, 61°45'35.9994"W; 9 November 2003)

7: Lance aux Epines, beach (12°0'7.2"N, 61°45'32.4"W; 9 November 2003)

8: The Lime, around apartment grounds (12°1'8.4"N, 61°45'39.6"; 9 November 2003)

9: Grand Anse, beach (12°1'19.2", 61°46'8.3994"W; 9 November 2003)

10: St. George's, Botanical Garden (12°2'49.2"N, 61°44'41.9994"W; 9 November 2003)

11: Annandale Waterfall, near falls (12°5'13.1994"N, 61°43'4.8"W; 9 November 2003)

12–13: Grand Etang, Morne La Baye (12°5'38.3994"N, 61°41'38.4"W; 9 November 2003)

14: Grand Etang, Park Centre (12°5'38.3994"N, 61°41'42"W; 9 November 2003)

15 and 40: Grand Etang Lake, south shore (12°5'42"N, 61°41'56.3994"W; 9 and 12 November 2003)

16: Grenville, around building (12°7'40.8"N, 61°37'30"W; 10 November 2003)

17: Peggy's Whim, secondary forest (12°10'30"N, 61°38'20.4"W; 10 November 2003)

18–19: Bathway Beach, sea grape and grass (12°12'21.5994"N, 61°36'46.7994"W; 10 November 2003)

20–21: Levera Bay, beachfront (12°13'29.9994"N, 61°36'43.2"W; 10 November 2003)

22: Levera NP, dry leaves in overhang (12°13'1.2"N, 61°36'46.7994"W; 10 November 2003)

23: Grand Mal, garden (12°4'44.4"N, 61°45'18"W; 10 November 2003)

24: Grand Anse, park at intersection (12°1'22.7994"N, 61°45'35.9994"W; 11 November 2003)

26: Grand Etang, tower by 1910 summit (12°5'6"N, 61°41'52.8"W; 11 November 2003)

27: Crochu, gas station (12°3'50.4"N, 61°38'49.1994"W; 11 November 2003)

28: Baillie's Bacolet, secondary forest (12°1'40.8"N, 61°41'9.5994"W; 11 November 2003)

29: Point Salines, beach (12°0'21.6"N, 61°47'52.8"W; 11 November 2003)

30–32: Coral Cove, mangrove (11°59'41.9994"N, 61°45'25.1994"W; 11 November 2003)

33–36: Concord waterfall, secondary forest (12°7'4.8"N, 61°43'11.9994"W; 12 November 2003)

37: Gouyave, beachfront (12°10'4.7994"N, 61°43'44.3994"W; 12 November 2003)

38: Castaigne (12°7'37.2"N, 61°40'29.9994"W; 12 November 2003)

39: Grand Etang, 0.8 km NE visitor centre (12°5'42"N, 61°41'42"W; 12 November 2003)

41: Paddock, by the lagoon (12°2'34.7994"N, 61°44'49.1994"W; 12 November 2003)

#### **Endeman, 12 January 2005 (four sites)**

F2: Gouyave, nutmeg factory (12°10'1.1994"N, 61°43'51.6"W; 12 January 2005)

F3: Grand Etang Lake, by restaurant (12°5'38.3994"N, 61°41'38.4"W; 12 January 2005)

F4: St. George's, by new pier (12°3'3.6"N, 61°45'21.6"W; 12 January 2005)

F5: Annandale Falls, by falls (12°5'13.1994"N, 61°43'1.1994"; 12 January 2005)

#### **Wetterer, 23–29 June 2006 (37 sites)**

462: Florida, 0.5 km E of town (12°9'32.4"N, 61°42'3.6"W; 23 June 2006)

463–465: Mt. Granby, end of road (12°8'9.5994"N, 61°43'8.4"W; 23 June 2006)

466–467: Richmond, top of hill (12°6'7.2"N, 61°44'2.4"W; 23 June 2006)

468–480: Mont D'Or, 1 km downhill (12°6'21.5994"N, 61°44'9.5994"W; 23 June 2006)

481: Bylands, by waterworks (12°8'16.7994"N, 61°39'35.9994"W; 24 June 2006)

482–484: Mt. Hope, 1.2 km up road (12°8'52.7994"N, 61°39'35.9994"W; 24 June 2006)

485–489: Grand Etang, 1.9 km SW of center (12°4'55.2"N, 61°42'3.6"W; 24 June 2006)

490–493: Black Forest, W border of reserve (12°4'51.5994"N, 61°42'28.7994"W; 24 June 2006)

494–496: Grand Anse, Shopping Centre (12°1'22.7994"N, 61°45'18"W; 24 June 2006)

497–499: Grand Anse, Allamanda Resort (12°1'30"N, 61°45'43.2"W; 24 June 2006)

500: Lake Antoine, NE track (12°11'13.1994"N, 61°36'54"W; 25 June 2006)

501–503: River Antoine, sugarcane field (12°10'30"N, 61°36'32.4"W; 25 June 2006)

504: Levera Estate, suburban shrubs (12°12'36"N, 61°37'4.8"W; 25 June 2006)

505: Sauteurs Bay, beach (12°13'44.3994"N, 61°39'3.6"W; 25 June 2006)

506: Mt. Alexandra, cacao (12°13'51.5994"N, 61°39'35.9994"W; 25 June 2006)

507–516: Crayfish Bay, SW Nonpareil (12°12'36"N, 61°41'38.4"W; 25 June 2006)

- 517–521: Tufton Hall, 1.2 km above fork (12°10'30"N, 61°41'38.4"W; 26 June 2006)
- 522–527: Mt. Nelson, 1.6 km above fork (12°10'33.6"N, 61°41'16.8"W; 26 June 2006)
- 528–530: Diamond Estate, 0.4 km below fork (12°11'2.3994"N, 61°42'3.6"W; 26 June 2006)
- 531–535: True Blue, by vet hospital (12°0'14.3994"N, 61°46'22.8"W; 26 June 2006)
- 536: True Blue, beach NW of point (11°59'52.7994"N, 61°46'4.8"W; 26 June 2006)
- 537: Woburn, sugarcane field (12°1'22.7994"N, 61°44'5.9994"W; 26 June 2006)
- 538: Marquis, beach (12°5'49.1994"N, 61°37'37.2"W; 27 June 2006)
- 539–547: Hope Estate, forest patch (12°4'40.7994"N, 61°38'2.4"W; 27 June 2006)
- 548–549: Apres Tout, fields above town (12°3'28.7994"N, 61°40'22.8"W; 27 June 2006)
- 550: Parade, suburban bus stop (12°3', 61°44'13.2"W; 27 June 2006)
- 551: Grand Anse, in hotel room (12°1'30"N, 61°45'43.2"W; 27 June 2006)
- 552: Woodlands, cane by factory (12°1'30"N, 61°44'27.5994"W; 28 June 2006)
- 553–556: Fort Jeudy, near entrance (12°0'46.7994"N, 61°43'4.8"W; 28 June 2006)
- 557–561: Fort Jeudy Point, open area at point (11°59'41.9994"N, 61°42'39.5994"W; 28 June 2006)
- 562: Petit Bacaye, wooded yard (12°1'15.6"N, 61°41'42"W; 28 June 2006)
- 563: Queen's Park, by forestry office (12°3'43.1994"N, 61°45'14.3994"W; 28 June 2006)
- 564–568: St. Margaret, E edge of reserve (12°6'10.7994"N, 61°40'55.2"W; 29 June 2006)
- 569–571: St. James, abandoned nursery (12°7'26.4"N, 61°39'53.9994"W; 29 June 2006)
- 572: Grenville, destroyed church (12°7'4.8"N, 61°37'37.2"W; 29 June 2006)
- 573–578: St. Margaret, 0.6 km above falls (12°5'45.6"N, 61°41'9.5994"W; 29 June 2006)
- 579, 580: Grand Etang, by tree nursery (12°4'58.8"N, 61°42'14.4"W; 29 June 2006)
- Wetterer, 2–9 July 2014 (39 sites)**
- 203–207: Quarantine Point, picnic area (12°1'26.3994"N, 61°46'29.9994"W; 2 July 2014)
- 208: Tempe, urban weeds (12°3'32.3994"N, 61°44'31.1994"W; 2 July 2014)
- 209–212: Mardigras, secondary forest (12°2'56.3994"N, 61°42'43.2"W; 2 July 2014)
- 213–214: Beaton, agriculture (12°2'6"N, 61°41'45.5994"W; 2 July 2014)
- 215–216: Westerhall, secondary forest (12°1'11.9994"N, 61°42'3.6"W; 2 July 2014)
- 217: Morne Rouge, hotel bathroom (12°1'15.6"N, 61°46'15.6"W; 3 July 2014)
- 218: Grand Etang NP, Mt. Qua Qua trail (12°5'42"N, 61°41'49.2"W; 3 July 2014)
- 219–226: Grand Etang NP, Beausejour Lookout (12°5'38.3994"N, 61°41'52.8"W; 3 July 2014)
- 227–238: Grand Etang NP, Mt. Qua Qua trail (12°6'3.6"N, 61°42'7.1994"W; 3 July 2014)
- 239: Morne Jaloux, wrecked house (12°1'44.3994"N, 61°44'13.2"W; 4 July 2014)
- 240–249: Morne Jaloux, plant nursery (12°1'58.7994"N, 61°43'55.1994"W; 4 July 2014)
- 250–255: Grand Etang NP, below tree nursery (12°4'55.2"N, 61°42'17.9994"W; 4 July 2014)
- 256–257: Morne Rouge, hotel grounds (12°1'15.6"N, 61°46'19.1994"W; 4 July 2014)
- 258–259: Soubise, beach (12°6'32.3994"N, 61°37'37.2"W; 5 July 2014)
- 260–265: Soubise, forest by waterfall (12°6'32.3994"N, 61°38'9.6"W; 5 July 2014)
- 266: Soubise, trail to waterfall (12°6'32.3994"N, 61°37'51.6"W; 5 July 2014)
- 267–268: Hope, by buildings (12°4'19.1994"N, 61°37'48"W; 5 July 2014)
- 269–271: Crochu, by zoo (12°3'17.9994"N, 61°38'2.4"W; 5 July 2014)
- 272: Crochu, roadside (12°3'32"N, 61°38'27.5994"W; 5 July 2014)
- 273–277: Tanteen, by Union Building (12°2'49.2"N, 61°44'52.7994"W; 6 July 2014)
- 278: St. George's, SE Carenage (12°3'N, 61°45'W; 6 July 2014)
- 279: St. George's, SW Carenage (12°2'56.3994"N, 61°45'10.8"W; 6 July 2014)
- 280: St. George's, Fort George (12°3'N, 61°45'14.3994"W; 6 July 2014)
- 281–282: St. George's, Melville St. (12°3'25.2"N, 61°45'14.3994"W; 6 July 2014)
- 283: Sans Souci, riverside (12°3'28.7994"N, 61°44'41.9994"W; 6 July 2014)
- 284–287: Port Louis, by entrance (12°2'34.7994"N, 61°45'; 6 July 2014)
- 288: St. George's, Hugh St. lot (12°3'10.8"N, 61°44'56.4"W; 6 July 2014)
- 289–295: Paraclete, by ballfield (12°8'56.3994"N, 61°38'49.1994"W; 7 July 2014)
- 296–300: Mt. St. Catherine, by towers (12°9'53.9994"N, 61°39'43.1994"W; 7 July 2014)
- 301: Mt. St. Catherine, trail (12°9'50.3994"N, 61°39'53.9994"W; 7 July 2014)
- 302–304: Paradise, by ballfield (12°7'58.7994"N, 61°39'53.9994"W; 7 July 2014)
- 305: Secret Harbour, marina (12°0'14.3994"N, 61°45'10.8"W; 8 July 2014)
- 306–307: Mt. Hartman, scrub (12°0'32.4"N, 61°45'3.5994"W; 8 July 2014)
- 308: Hog Island, by bridge (12°0'14.3994"N, 61°44'20.3994"W; 8 July 2014)
- 309: Hog Island, near middle (12°0'14.3994"N, 61°44'20.3994"W; 8 July 2014)
- 310: Hog Island, by Roger's bar (12°0'14.3994"N, 61°44'20.3994"W; 8 July 2014)

311–315: Avocet, 0.4 km N of dam (12°4'8.4"N, 61°42'3.5"W; 9 July 2014)  
 316–319: Avocet, just N of reservoir (12°3'57.6"N, 61°42'3.6"W; 9 July 2014)  
 320–322: Avocet, 0.6 km S of dam (12°3'32.3994"N, 61°42'; 9 July 2014)

#### Mancini, 18–19 April 2015 (five sites)

119: Carriacou, Anse La Roche (12°31'4.8"N, 61°26'49.2"W; 18 April 2015)  
 120: Carriacou, Tyrrel Bay (12°27'14.4"N, 61°29'5.9994"W; 18 April 2015)  
 121–123: Nonpareil (12°12'39.6"N, 61°41'27.6"W; 18 April 2015)  
 124: Levera Pond, red mangrove (12°13'8.3994"N, 61°36'39.5994"W; 19 April 2015)  
 125: Bathway Bay (12°12'46.7994"N, 61°36'35.9994"W; 19 April 2015)

#### LITERATURE CITED

- Baroni-Urbani, C., and E. O. Wilson. 1987. The fossil members of the ant tribe Leptomyrmecini (Hymenoptera: Formicidae). *Psyche* 94: 1–8.
- Bolton, B. 1979. The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Malagasy region and in the New World. *Bulletin of the British Museum (Natural History) Entomology* 38: 129–181.
- Bolton, B. 1987. A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History) Entomology* 54: 263–452.
- Bolton, B. 2000. The ant tribe Dacetini. *Memoirs of the American Entomological Institute* 65: 1–1028.
- Bolton, B. 2018a. *Camponotus sexguttatus*. AntCat: an online catalog of ants of the world. Available from: [www.antcat.org/catalog/433734](http://www.antcat.org/catalog/433734)
- Bolton, B. 2018b. *Camponotus sexguttatus biguttatus*. AntCat: an online catalog of ants of the world. Available from: [www.antcat.org/catalog/432123](http://www.antcat.org/catalog/432123)
- Bolton B., and B. L. Fisher. 2011. Taxonomy of Afrotropical and West Palaearctic ants of the ponerine genus *Hypoponera* Santschi (Hymenoptera: Formicidae). *Zootaxa* 2843: 1–118.
- Brandão, C. R. F., J. L. M. Diniz, and E. M. Tomotake. 1991. *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insectes Sociaux* 38: 335–344.
- Brown, W. L., Jr. 1959. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: group of *gundlachi* (Roger). *Psyche* 66: 37–52.
- Brown, W. L., Jr. 1960. Contributions toward a reclassification of the Formicidae. III. Tribe Amblyoponini (Hymenoptera). *Bulletin of the Museum of Comparative Zoology* 122: 143–230.
- Brown, W. L., Jr. 1962. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: synopsis and keys to species. *Psyche* 69: 238–267.
- Brown, W. L., Jr. 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cyldromyrmecini, Acanthostichini, and Aenictogitini. *Search Agriculture* 5: 1–115.
- Brown, W. L., Jr. 1976. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomologica* 19: 67–171.
- Carlquist, S. 1965. *Island Life. A Natural History of the Islands of the World*. New York: Natural History Press.
- Castles, J. 1790. Observations on the Sugar Ants. In a Letter from John Castles, Esq. to Lieut. Gen. Melvill, F.R.S. *Philosophical Transactions of the Royal Society of London* 80: 688–694.
- Creighton, W. S. 1930. The New World species of the genus *Solenopsis* (Hymenop. Formicidae). *Proceedings of the American Academy of Arts and Sciences* 66(2): 39–151.
- De Andrade, M. L., and C. Baroni Urbani. 1999. Diversity and adaptation in the ant genus *Cephalotes*, past and present. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 271: 1–889.
- Deyrup, M. 1991. *Technomyrmex albipes*, a new exotic ant in Florida (Hymenoptera: Formicidae). *Florida Entomologist* 74: 147–148.
- Deyrup, M. 2003. An updated list of Florida ants (Hymenoptera: Formicidae). *Florida Entomologist* 86: 43–48.
- Deyrup, M. 2016. *Ants of Florida. Identification and Natural History*. Boca Raton: CRC Press.
- Deyrup, M., L. Davis, and S. Buckner. 1998. Composition of the ant fauna of three Bahamian Islands, PP. 23–31 IN: T. K. Wilson, editor. *Proceedings of the Seventh Symposium on the Natural History of the Bahamas*. San Salvador: Bahamian Field Station.
- Deyrup, M., L. Davis, and S. Cover. 2000. Exotic ants in Florida. *Transactions of the American Entomological Society* 126: 293–326.
- Deyrup, M., J. Trager, and N. Carlin. 1985. The genus *Odontomachus* in the southeastern United States (Hymenoptera: Formicidae). *Entomological News* 96: 188–195.
- DuBois, M. B. 1986. A revision of the native New World species of the ant genus *Monomorium* (minimum group) (Hymenoptera: Formicidae). *University of Kansas Science Bulletin* 53: 65–119.

- Duncan, R. A., and R. B. Hargraves. 1984. Plate tectonic evolution of the Caribbean region in the mantle reference frame, PP. 81–93 IN: W. E. Bonini, R. B. Hargraves, and R. Shagam, editors. *The Caribbean–South American Plate Boundary and Regional Tectonics*. Boulder, Colorado: Geological Society of America.
- Emery, C. 1892. Voyage de M. Ch. Alluaud dans le territoire d'Assinie (Afrique occidentale) en juillet et août 1886. Formicides. *Annales de la Société Entomologique de France* 60: 553–574.
- Emery, C. 1898. Aggiunte e correzioni al saggio di un catalogo sistematico dei generi *Camponotus*, *Polyrhachis* e affini. *Rendiconti delle Sessioni della Reale Accademia delle Scienze dell'Istituto di Bologna* 2: 225–231.
- Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. *Genera Insectorum* 118: 1–125.
- Emery, C. 1925. Hymenoptera, Fam. Formicidae, Subfam. Formicinae. *Genera Insectorum* 183: 1–302.
- Escarraga, M., and R. J. Guerrero. 2016. The ant genus *Linepithema* (Formicidae: Dolichoderinae) in Colombia. *Zootaxa*. 4208(5):zootaxa.4208.5.3. doi: 10.11646/zootaxa.4208.5.3
- Feitosa, R. M., and C. R. F. Brandão. 2008. A taxonomic revision of the Neotropical myrmicine ant genus *Lachnomyrmex* Wheeler (Hymenoptera: Formicidae). *Zootaxa* 1890: 1–49.
- Forel, A. 1893. Formicides de l'Antille St. Vincent. Récoltées par Mons. H. H. Smith. *Transactions of the Entomological Society of London* 1893(4): 333–418.
- Forel, A. 1897. Quelques Formicides de l'Antille de Grenada récoltés par M. H. H. Smith. *Transactions of the Entomological Society of London* 1897: 297–300.
- Forel, A. 1909. Ameisen aus Guatemala usw., Paraguay und Argentinien (Hym.). *Deutsche Entomologische Zeitschrift* 1909: 239–269.
- Forel, A. 1912. Formicides Néotropiques. Part III. 3me sous-famille Myrmicinae (suite). Genres *Crematogaster* et *Pheidole*. *Memoires de la Société Entomologique de Belgique* 19: 211–237.
- Gotzek, D., S. G. Brady, R. J. Kallal, and J. S. LaPolla. 2012. The importance of using multiple approaches for identifying emerging invasive species: the case of the Raspberry crazy ant in the United States. *PLoS ONE* 7(9): e45314. doi: 10.1371/journal.pone.0045314
- Hashmi, A. A. 1973. A revision of the Neotropical ant subgenus *Myrmothrix* of genus *Camponotus* (Hymenoptera: Formicidae). *Studia Entomologica* 16: 1–140.
- Hedges, S. B. 2001. Biogeography of the West Indies: an overview, PP. 15–33 IN: C. A. Woods and F. E. Sergile, editors. *Biogeography of the West Indies. Patterns and Perspectives*. New York: CRC Press.
- Jahyny, B., H. S. R. Alves, D. Fresneau, and J. H. C. Delabie. 2015. Estudos biogeográficos sobre o gênero *Thaumatomyrmex* Mayr, 1887 (Ponerinae, Ponerini), PP. 327–343 IN: J. H. C. Delabie, R. M. Feitosa, J. E. Serrão, C. S. F. Mariano, and J. D. Majer, editors. *As Formigas Poneromorfas do Brasil*. Ilhéus: Editus.
- Kempf, W. W. 1960. Estudo sobre *Pseudomyrmex* I. (Hymenoptera: Formicidae). *Revista Brasileira de Entomologia* 9: 5–32.
- Kempf, W. W. 1972. Catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). *Studia Entomologica* 15: 3–344.
- Klingenberg, C., C. R. F. Brandão, and W. Engels. 2007. Primitive nest architecture and small monogynous colonies in basal Attini inhabiting sandy beaches of southern Brazil. *Studies on Neotropical Fauna and Environment* 42: 121–126.
- Kouakou, L. M. M., W. Dekoninck, M. Kone, T. Delsinne, K. Yeo, K. Ouattara, and S. Konate. 2018. Diversity and distribution of introduced and potentially invasive ant species from the three main ecoregions of Côte d'Ivoire (West Africa). *Belgian Journal of Zoology* 148: 83–103.
- Kugler, C. 1994. A revision of the ant genus *Rogeria* with description of the sting apparatus (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* 3: 17–89.
- LaPolla, J. S., and J. Sosa-Calvo. 2006. Review of the ant genus *Rogeria* (Hymenoptera: Formicidae) in Guyana. *Zootaxa* 1330: 59–68.
- Lattke, J. E. 2011. Revision of the New World species of the genus *Leptogenys* Roger (Insecta: Hymenoptera: Formicidae: Ponerinae). *Arthropod Systematics and Phylogeny* 69(3): 127–264.
- Longino, J. T. 2003. The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa* 151: 1–150.
- Longino, J. T., and F. Fernández C. 2007. A taxonomic review of the genus *Wasmannia*. *Memoirs of the American Entomological Institute* 80: 271–289.
- Lubertazzi, D. 2019. The ants of Hispaniola. *Bulletin of the Museum of Comparative Zoology* 162(2): (1 April 2019). <https://doi.org/10.3099/MCZ-43.1>.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, New Jersey: Princeton Univ. Press.
- MacGown, J. A., B. Boudinot, M. Deyrup, and D. M. Sorger. 2014. A review of the Nearctic *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) with a treatment of the males. *Zootaxa* 3802: 515–552.
- MacGown, J. A., and J. K. Wetterer. 2013. Distribution and biological notes of *Strumigenys margaritae* (Hymenoptera: Formicidae: Dacetini). *Terrestrial Arthropod Reviews* 6: 247–255.



- MacGown, J. A., J. K. Wetterer, and J. G. Hill. 2012. Geographic spread of *Strumigenys silvestrii* (Hymenoptera: Formicidae: Dacetini). *Terrestrial Arthropod Reviews* 5: 213–222.
- Mackay, W. P., and E. Mackay. 2010. *The Systematics and Biology of the New World Ants of the Genus Pachycondyla* (Hymenoptera: Formicidae). Lewiston, New York: Edwin Mellen Press.
- Pacheco, J. A., and W. Mackay. 2013. *The Systematics and Biology of the New World Thief Ants of the Genus Solenopsis* (Hymenoptera: Formicidae). Lampeter, Wales: Edwin Mellen Press.
- Peterson, C. E. 1973. Sawdust trail, annals of sawmilling and the lumber trade from Virginia to Hawaii via Maine, Barbados, Sault Ste. Marie, Manchac and Seattle to the year 1860. *Bulletin of the Association for Preservation Technology* 5: 84–153.
- Pindell, J. L., and S. F. Barrett. 1990. Geological evolution of the Caribbean region; a plate-tectonic perspective, PP. 405–432 IN: G. Dengo and J. E. Case, editors. *The Caribbean Region*. Boulder, Colorado: Geological Society of America.
- Rabeling, C., M. Verhaagh, and W. Engels. 2007. Comparative study of nest architecture and colony structure of the fungus-growing ants, *Mycocepurus goeldii* and *M. smithii*. *Journal of Insect Science* 7(40): 1–13.
- Risch, S. J., and C. R. Carroll. 1982. Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology* 63: 1979–1983.
- Schmidt, C. A., and S. O. Shattuck. 2014. The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa* 3817: 1–242.
- Seal, J. N., K. Kellner, A. Trindl, and J. Heinze. 2011. Phylogeography of the parthenogenic ant *Platythyrea punctata*: highly successful colonization of the West Indies by a poor disperser. *Journal of Biogeography* 38: 868–882.
- Seifert, B. 2003. The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae). A taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi*, and *C. minutior* species groups. *Annalen des Naturhistorischen Museums in Wien Serie B Botanik und Zoologie* 104 B: 203–338.
- Shuckard, W. E. 1840. Monograph of the Dorylidae, a family of the Hymenoptera Heterogyna. *Annals and Magazine of Natural History* 5: 258–271.
- Smiley, C. J. 2002. Lower Cretaceous plants from the Dominican Republic, PP. 119–129 IN: T. A. Jackson, editor. *Caribbean Geology into the Third Millennium*. Kingston, Jamaica: University of the West Indies Press.
- Smith, M.R. 1936. Ants of the genus *Ponera* in America, North of Mexico. *Annals of the Entomological Society of America* 29: 420–430.
- Snelling, R. R., and J. A. Torres. 1998. *Camponotus ustus* Forel and two similar new species from Puerto Rico (Hymenoptera: Formicidae). *Contributions in Science (Los Angeles)* 469: 1–10.
- Solórzano, L. A., S. McKenna, and K. Walker. 2005. The Caribbean Biodiversity Initiative at Conservation International, PP. 299–302 IN: P. Milosavlitch, and E. Klein, editors. *Caribbean Marine Biodiversity: The Known and the Unknown*. Lancaster, Pennsylvania: Destech Publications.
- Taylor, R. W., and E. O. Wilson. 1962. Ants from three remote oceanic islands. *Psyche* 68: 137–144.
- Torres, J. A., and R. R. Snelling. 1997. Biogeography of Puerto Rican ants: a non-equilibrium case? *Biodiversity and Conservation* 6: 1103–1121.
- Trager, J. C. 1984. A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. *Sociobiology* 9: 49–162.
- Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *Journal of the New York Entomological Society* 99: 141–198.
- Ward, P. S. 1992. Ants of the genus *Pseudomyrmex* (Hymenoptera: Formicidae) from Dominican amber, with a synopsis of the extant Antillean species. *Psyche* 99: 55–85.
- Wetterer, J. K. 2007. Biology and impacts of Pacific islands invasive species. 3. The African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Pacific Science* 61: 437–456.
- Wetterer, J. K. 2008. Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). *Myrmecological News* 11: 137–149.
- Wetterer, J. K. 2009a. Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae). *Myrmecological News* 12: 23–33.
- Wetterer, J. K. 2009b. Worldwide spread of the destroyer ant, *Monomorium destructor* (Hymenoptera: Formicidae). *Myrmecological News* 12: 97–108.
- Wetterer, J. K. 2009c. Worldwide spread of the penny ant, *Tetramorium bicarinatum* (Hymenoptera: Formicidae). *Sociobiology* 54: 811–830.
- Wetterer, J. K. 2010. Worldwide spread of the flower ant, *Monomorium floricola* (Hymenoptera: Formicidae). *Myrmecological News* 13: 19–27.
- Wetterer, J. K. 2011a. Worldwide spread of *Pheidole teneriffana* (Hymenoptera: Formicidae). *Florida Entomologist* 94: 843–847.
- Wetterer, J. K. 2011b. Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenop-

- tera: Formicidae). *Myrmecological News* 14: 21–35.
- Wetterer, J. K. 2012a. Worldwide spread of Roger's dacetine ant, *Strumigenys rogeri* (Hymenoptera: Formicidae). *Myrmecological News* 16: 1–6.
- Wetterer, J. K. 2012b. Worldwide spread of the stigma ant, *Pachycondyla stigma* (Hymenoptera: Formicidae). *Myrmecological News* 16: 39–44.
- Wetterer, J. K. 2012c. Worldwide spread of Emma's dacetine ant, *Strumigenys emmae* (Hymenoptera: Formicidae). *Myrmecological News* 16: 69–74.
- Wetterer, J. K. 2012d. Worldwide spread of Emery's sneaking ant, *Cardiocondyla emeryi* (Hymenoptera: Formicidae). *Myrmecological News* 17: 13–20.
- Wetterer, J. K. 2012e. Worldwide spread of the Moorish sneaking ant, *Cardiocondyla mauritanica* (Hymenoptera: Formicidae). *Sociobiology* 59: 985–997.
- Wetterer, J. K. 2012f. Worldwide spread of the African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Myrmecological News* 17: 51–62.
- Wetterer, J. K. 2013a. Worldwide spread of the little fire ant, *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Terrestrial Arthropod Reviews* 6: 173–184.
- Wetterer, J. K. 2013b. Exotic spread of *Solenopsis invicta* (Hymenoptera: Formicidae) beyond North America. *Sociobiology* 60: 53–63.
- Wetterer, J. K. 2014a. Worldwide spread of Alluaud's little yellow ant, *Plagiolepis alluaudi* (Hymenoptera: Formicidae). *Myrmecological News* 19: 53–59.
- Wetterer, J. K. 2014b. Worldwide spread of the lesser sneaking ant, *Cardiocondyla minutior* (Hymenoptera: Formicidae). *Florida Entomologist* 97: 567–574.
- Wetterer, J. K. 2016. Geographic range of *Pachycondyla harpax* (Hymenoptera, Formicidae). *Sociobiology* 63: 623–627.
- Wetterer, J. K. 2017. Geographic distribution of *Monomorium ebeninum* (Hymenoptera, Formicidae). *Transactions of the American Entomological Society* 143: 703–710.
- Wetterer, J. K. 2018. Geographic distributions of *Strumigenys gundlachi* and *Strumigenys eggersi* (Hymenoptera, Formicidae). *Transactions of the American Entomological Society* 144: 131–141.
- Wetterer, J. K. (in press). Geographic spread of *Solenopsis globularia* (Hymenoptera: Formicidae). *Sociobiology*.
- Wetterer, J. K., O. Davis, and J. R. Williamson. 2014. Boom and bust of the tawny crazy ant, *Nylanderia fulva*, on St. Croix, US Virgin Islands. *Florida Entomologist* 97: 1099–1103.
- Wetterer, J. K., M. A. Deyrup, and A. Bryant. 2018. Spread of the non-native trap-jaw ant *Anochetus mayri* (Hymenoptera: Formicidae) in Florida. *Transactions of the American Entomological Society* 144: 437–441.
- Wetterer, J. K., X. Espadaler, P. Ashmole, C. Cutler, and J. Endeman. 2007. Ants (Hymenoptera: Formicidae) of the South Atlantic islands of Ascension Island, St Helena, and Tristan da Cunha. *Myrmecological News* 10: 29–37.
- Wetterer, J. K., and R. J. Guerrero. 2017. Geographic distribution of *Tapinoma litorale* (Hymenoptera: Formicidae). *Florida Entomologist* 100: 145–148.
- Wetterer, J. K., and J. L. W. Keularts. 2008. Population explosion of the hairy crazy ant, *Paratrechina pubens* (Hymenoptera: Formicidae), on St. Croix, US Virgin Islands. *Florida Entomologist* 91: 423–427.
- Wetterer, J. K., D. Lubertazzi, J. Rana, and E.O. Wilson. 2016. Ants of Barbados (Hymenoptera: Formicidae). *Breviora* 548: 1–34.
- Wetterer, J. K., and M. R. Sharaf. 2017. Worldwide distribution of *Sylophopsis sechellensis* (Hymenoptera: Formicidae). *Florida Entomologist* 100: 281–285.
- Wetterer, J. K., and A. L. Wetterer. 2004. Ants (Hymenoptera: Formicidae) of Bermuda. *Florida Entomologist* 87: 212–221.
- Wheeler, W. M. 1905. The ants of the Bahamas, with a list of the known West Indian species. *Bulletin of the American Museum of Natural History* 21: 79–135.
- Wheeler, W. M. 1908. The ants of Porto Rico and the Virgin Islands. *Bulletin of the American Museum of Natural History* 24: 117–158.
- Wheeler, W. M. 1910a. Three new genera of myrmicine ants from tropical America. *Bulletin of the American Museum of Natural History* 28: 259–265.
- Wheeler, W. M. 1910b. *Ants: Their Structure, Development and Behavior*. New York: Columbia Univ. Press.
- Wheeler, W. M. 1911. Ants collected in Grenada, W. I., by C. T. Brues. *Museum of Comparative Zoology (Harvard College) Bulletin* 54: 167–172.
- Wheeler, W. M. 1923. Report on the ants collected by the Barbados–Antigua Expedition from the Univ. of Iowa in 1918. *Studies in Natural History, Iowa University* 10: 3–9.
- Wheeler, W. M. 1926. *The Natural History of Ants. From an unpublished manuscript in the archives of the Academy of Sciences of Paris by René Antoine Ferchault de Réaumur*. New York: Alfred A. Knopf.
- Wilcox, B. A. 1978. Supersaturated island faunas: a species–age relationship for lizards on post-Pleistocene land-bridge islands. *Science* 199: 996–998.
- Wild, A. L. 2007. Taxonomic revision of the ant genus *Linepithema* (Hymenoptera: Formicidae). *Uni-*

- versity of California Publications in Entomology* 126: 1–151.
- Wilson, E. O. 1954. The ecology of some North American dacetine ants. *Annals of the Entomological Society of America* 46: 479–495.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95: 169–193.
- Wilson, E. O. 1985a. Ants of the Dominican amber (Hymenoptera: Formicidae). 1. Two new Myrmicine genera and an aberrant Pheidole. *Psyche* 92: 1–9.
- Wilson, E. O. 1985b. Ants of the Dominican amber (Hymenoptera: Formicidae). 2. The first fossil army ants. *Psyche* 92: 11–16.
- Wilson, E. O. 1985c. Ants of the Dominican amber (Hymenoptera: Formicidae). 3. The subfamily Dolichoderinae. *Psyche* 92: 17–37.
- Wilson, E. O. 1985d. Ants of the Dominican amber (Hymenoptera: Formicidae). 4. A giant Ponerine in the genus *Paraponera*. *Israel Journal of Entomology* 19: 197–200.
- Wilson, E. O. 1985e. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science* 229: 265–267.
- Wilson, E. O. 1988. The biogeography of the West Indian ants (Hymenoptera: Formicidae), PP. 214–230 IN: J. K. Liebherr, editor. *Zoogeography of Caribbean Insects*. Ithaca, New York: Cornell Univ. Press.
- Wilson, E. O. 2003. *Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus*. Cambridge, Massachusetts: Harvard Univ. Press.
- Wilson, E. O. 2005. Early ant plagues in the New World. *Nature* 433: 32.
- Woodruff, R. E., B. M. Beck, P. E. Skelley, C. Y. L. Schotman, and M. C. Thomas. 1998. *Checklist and Bibliography of the Insects of Grenada and the Grenadines*. Gainesville, Florida: Sandhill Crane Press.
- WMO (World Meteorological Organization) 2005. Twenty-Seventh Session RA IV Hurricane Committee. Final Report. San José, Costa Rica: World Meteorological Organization.
- Worldpopulationreview.com 2018. Total population by country 2018. worldpopulationreview.com/countries/